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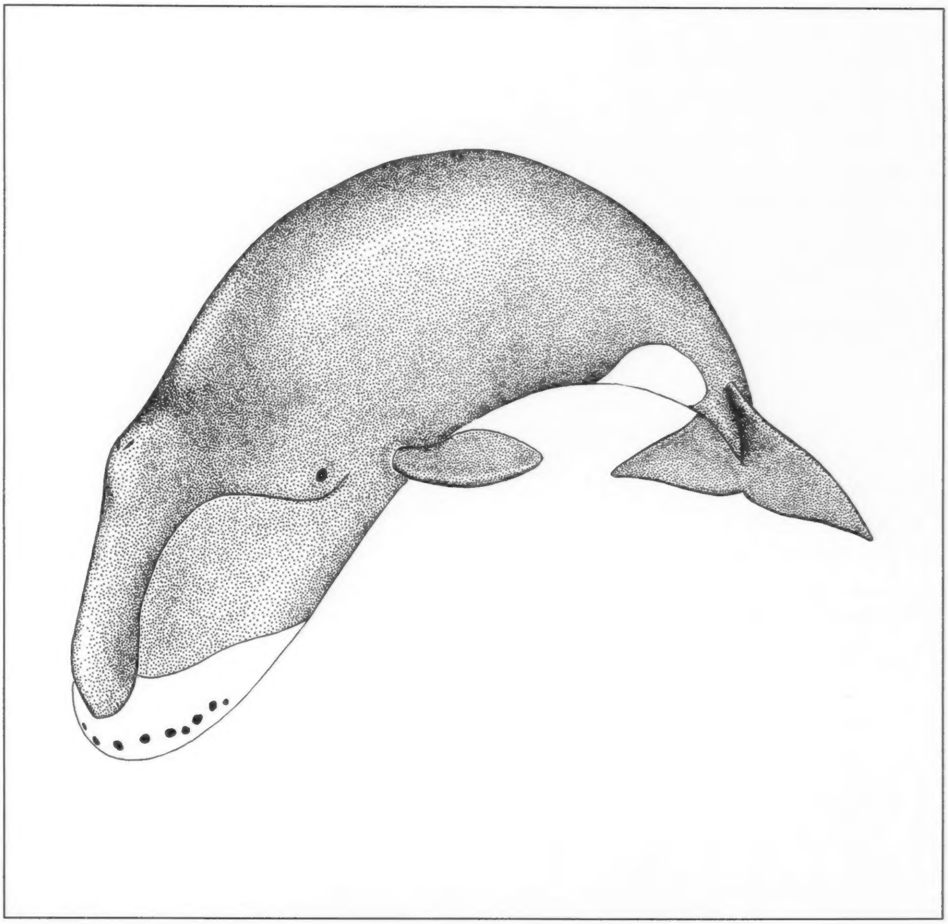
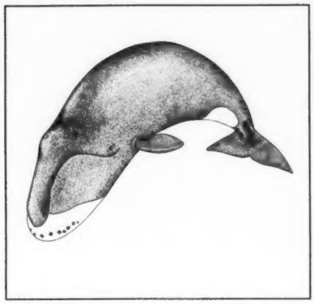


THE BOWHEAD WHALE

Marine Fisheries REVIEW



On the cover: a juvenile bowhead whale, *Balaena mysticetus*. NMFS illustration by David G. Stanton, SPO.

Articles 57(3-4), 1995

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The Bowhead Whale, *Balaena mysticetus*: Its Historic and Current Status

KIM E.W. SHELDEN and DAVID J. RUGH

Introduction

Bowhead whales, *Balaena mysticetus* (Fig. 1), are currently listed as endangered under the Endangered Species Act of 1973 (ESA) and depleted under the Marine Mammal Protection Act of 1972 (MMPA). The ESA, as amended in 1978, requires the status of populations listed as "endangered" or "threatened" to be reviewed every 5 years. For bowhead whales, an evaluation is to be made as to whether the status of these whales should be revised (i.e., changed to threatened) or whether specific stocks should be removed from the list of Endangered and Threatened Wildlife (50 C.F.R. § 17.11). This paper is an update of literature that has become available since the publication of Braham (1984) and a review of elements that may contribute to the evaluation of the status of stocks of bowhead whales.

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ABSTRACT—The bowhead whale, Balaena mysticetus, *is currently listed as endangered under the Endangered Species Act of 1973 and as depleted under the Marine Mammal Protection Act of 1972. Literature on the species is updated since 1984, and elements are reviewed that may contribute to the evaluation of the status of bowhead whale stocks.*

Background

Under the ESA, "endangered" status is designated to those species facing extinction "throughout all or a significant portion of [their] range. . . " (16 U.S.C. § 1532(6)). "Threatened" status is provided to ". . . any species which is likely to become an endangered species within the foreseeable future throughout all or a significant portion of its range" (16 U.S.C. § 1532(20)). The definition of species within the ESA is not based on the taxonomic categories used in the field of biology. Instead the term refers to ". . . any subspecies of fish or wildlife or plants, and any distinct population segment of any species of vertebrate fish or wildlife that interbreeds when mature" (16 U.S.C. § 1532(16)). Subspecies and distinct population segments are not defined within the statute. In 1992, the U.S. Fish and Wildlife Service (USFWS) issued a draft policy providing a definition for "distinct population segments," reviewed by Rohlf (1994). This policy was revised and published in the Federal Register (vol. 59, p. 65885) in 1994, and the final policy was published in 1996 (Fed. Regist., vol. 61, p. 4722). Within this policy, three elements will be considered in the status designation of population segments: 1) discreteness, 2) significance, and 3) conservation status.

Historically, the distribution of these whales was almost circumpolar in the northern hemisphere (Fig. 2); however, heavy exploitation by commercial whalers seriously depleted them throughout their range. For management purposes, five stocks (geographically distinct segments of the population) are currently recognized (IWC, 1992:27). Three of these stocks are found in the North At-

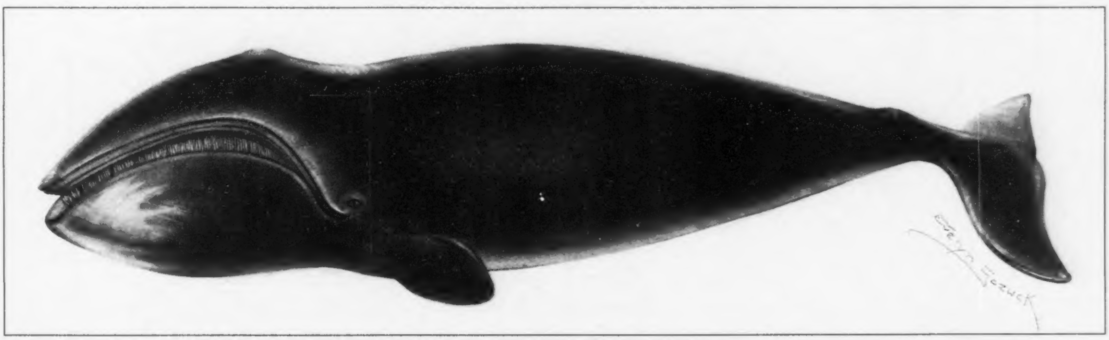

Figure 1. — The bowhead whale, *Balaena mysticetus.*

lantic and two in the North Pacific, some or all of which may be reproductively isolated.

Distribution and Abundance

Spitsbergen Stock

Commonly referred to as the Greenland whale, bowhead whales in the eastern North Atlantic have been observed in the waters north of Iceland and as far east as the Laptev Sea. Between 1940 and September 1990, 37 bowhead whale sightings have been recorded in this region, but some of these sightings were not unequivocally bowhead whales (Moore and Reeves, 1993:Table 9.2). Reviewing records from west to east, sightings were scattered along the coastline of Greenland, in the waters near Spitsbergen Island, off North Cape in northern Norway, in the waters of Zemlya Frantsa-losifa (Franz Josef Land), near Novaya Zemlya, and near Severnaya Zemlya (Fig. 3).

The majority of observations occurred between April and September. Overall, group sizes were small, ranging from 1 to 15 individuals, with the exception of two groups observed in August in Zemlya Frantsa-losifa, "sev-

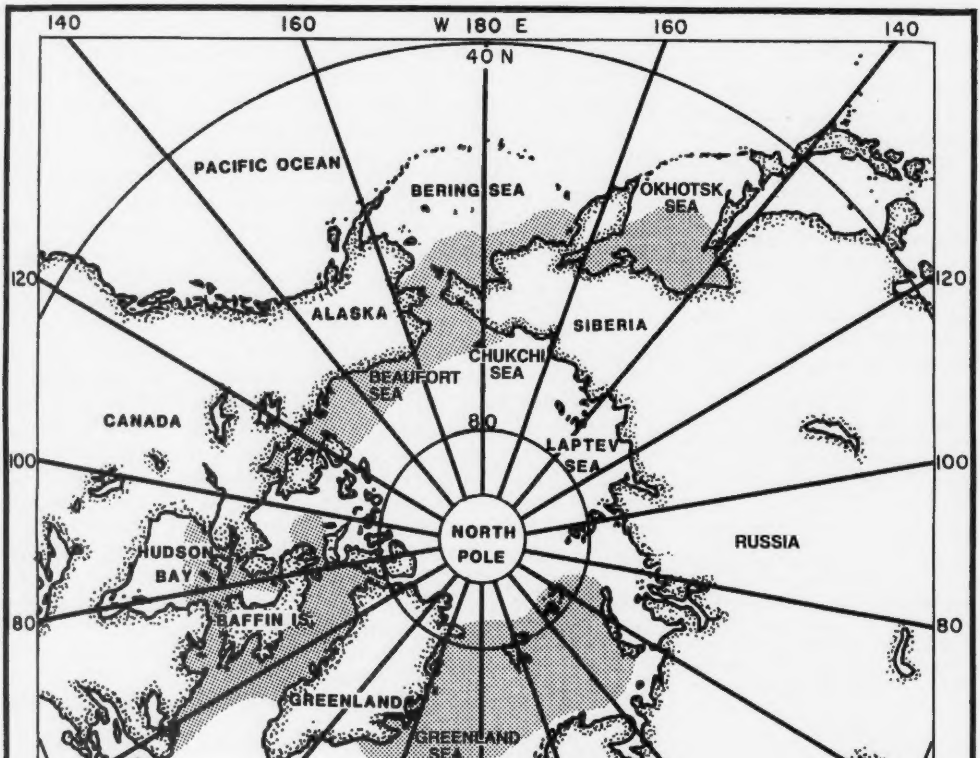

Figure 2. — Circumpolar distribution of bowhead whales (adapted from Reeves and Leatherwood, 1985).

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eral tens of whales" in 1981, and "about 66 individuals" in 1983 (Belikov et al., 1989:255). In 1989, Clark et al.[1] identified at least four bowhead whales from acoustic recordings collected off Spitsbergen. Additional sightings of lone animals were reported in each year during 1990–93 in Zemlya Frantsa-Iosifa (de Korte and Belikov, 1994). Despite extensive research cruises conducted in the Barents Sea (McQuaid, 1986), Icelandic waters (Sigurjónsson, 1985; Sigurjónsson et al., 1988; Sigurjónsson et al.[2]), Norwegian and adjacent waters (Christensen et al.[3]), and continued Danish and Norwegian whaling activity, very few bowhead whales have been seen. It may be that some of the Spitsbergen stock overwinter within the pack ice (Moore and Reeves, 1993), in regions inaccessible to unreinforced vessels. Bowhead whales observed from aircraft were often found in polynyas or leads within solid ice (Belikov et al., 1989).

Movement patterns of bowhead whales within the eastern North Atlantic are not well known. Whalers described the migration of animals hunted between Greenland and Spitsbergen Island as following a counterclockwise circuit (Southwell, 1898, as summarized in Ross, 1993). The whales would winter in the water near Iceland and Jan Mayen, then move northeastward as the ice front retreated during March and April. From May to June, the animals summered along the ice edge between Greenland and Spitsbergen before moving south again with the advancing pack ice. Variations in the routes taken during the southbound migration have been attributed to the existence of separate

[1] Clark, C. W., L. M. Brown, K. von der Heydt, A. Baggeroer, and I. Dyer. 1991. Acoustic detections of bowhead whales from the east Greenland–Spitsbergen stock in spring 1989. Int. Whal. Comm. Unpubl. Doc. SC/43/PS19, 12 p.

[2] Sigurjónsson, J., T. Gunnlaugsson, P. Ensor, M. Newcomer, and G. Vikingsson. 1990. North Atlantic sightings survey 1989 (NASS–89): shipboard surveys in Icelandic and adjacent waters July–August 1989. Int. Whal. Comm. Unpubl. Doc. SC/42/O21, 29 p.

[3] Christensen, I., T. Haug, and N. Øien. 1990. Review of the biology, exploitation and present abundance of large baleen whales and sperm whales in Norwegian and adjacent waters. Int. Whal. Comm. Unpubl. Doc. SC/42/105, 28 p.

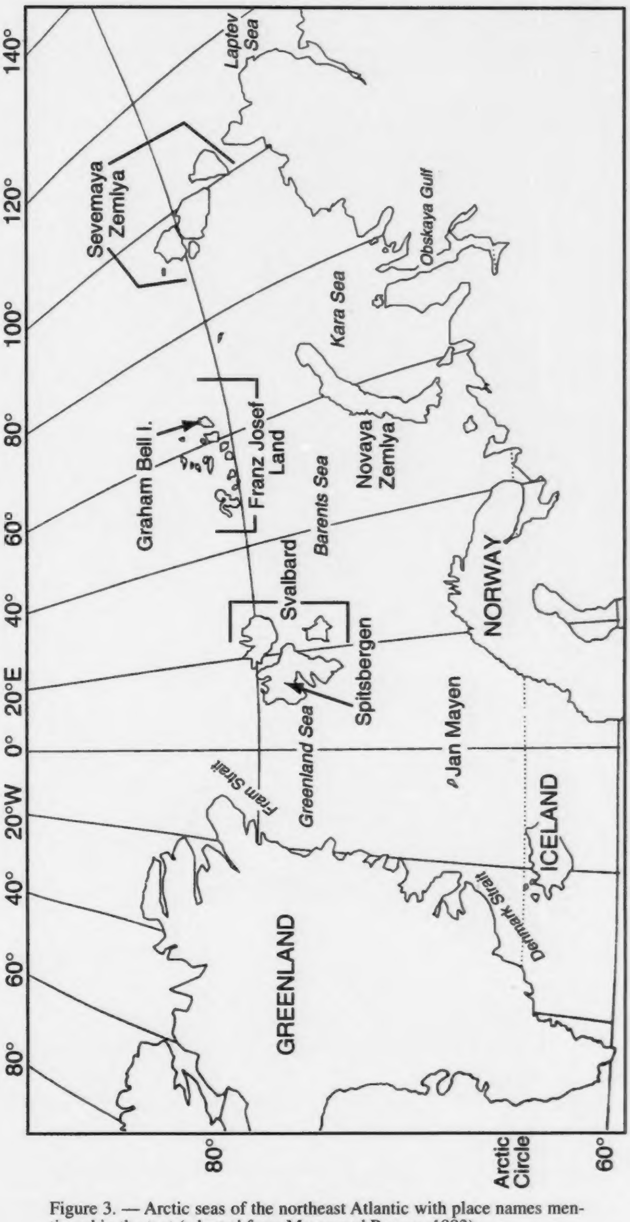
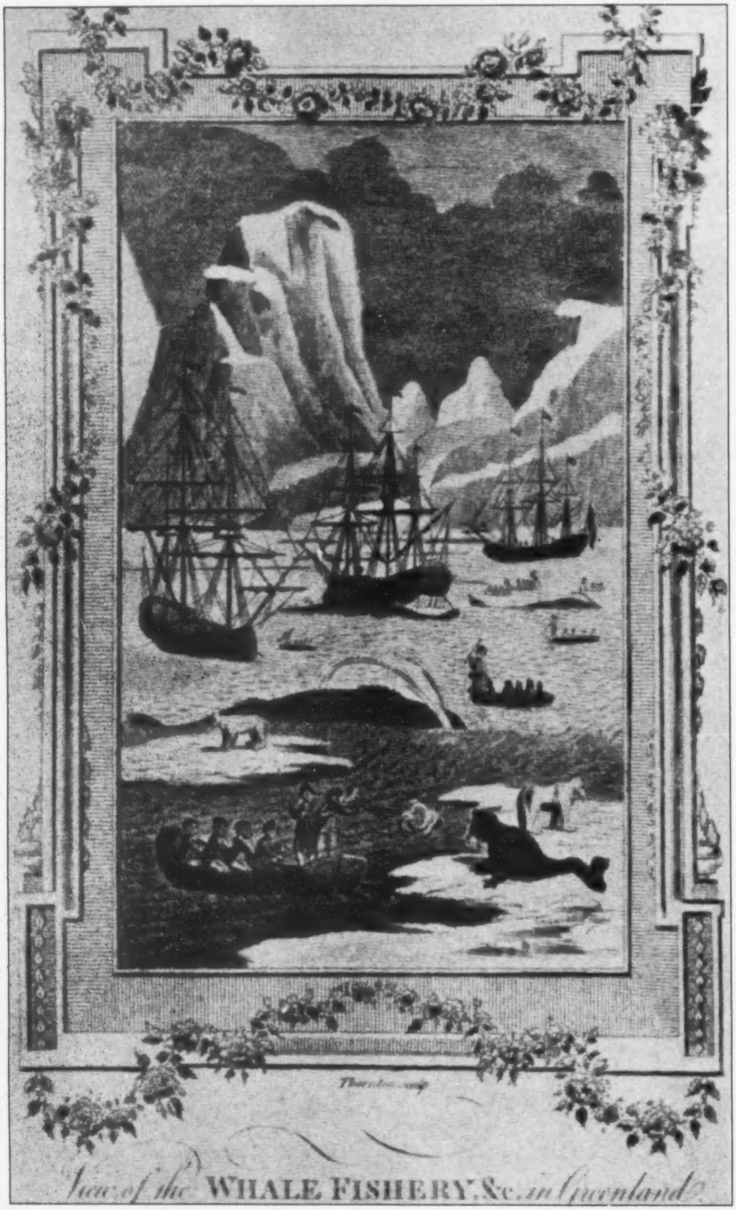


Figure 3. — Arctic seas of the northeast Atlantic with place names mentioned in the text (adapted from Moore and Reeves, 1993).

"tribes" (subspecies or species) of bowhead whales (Scoresby, 1820:211) or segregation of the population into age- or sex-specific groups (Southwell, 1898; de Jong, 1983).

Little is known of the migration patterns of bowhead whales found in the northern Barents Sea. Whalers described how a group of whales would arrive out of the east during heavy ice years to summer along the southern coast of Spitsbergen, then return east as the ice retreated (Zorgdrager, 1720, summarized in Eschricht and Reinhardt, 1866). These whales were said to look and behave differently from the other Spitsbergen whales. However, establishing the existence of any genetic or morphological variations between these groups would be difficult given the reduced size of the current population (Reeves, 1980).



The early whale fishery in Greenland is depicted in this 1781 engraving from Dow (1967), courtesy of and copyright by Argosy Book Store, Inc., N.Y.

There is some confusion as to whether the animals present in these waters today are representative of the historic stock. Jonsgård (1981, 1982) expressed the possibility that the Spitsbergen stock may be extinct. Past sightings may include migrants from the Davis Strait stock or the East Siberian Sea (Bering Sea stock) (Jonsgård, 1981). Whalers reported incidents in which "unsuccessfully harpooned" whales from one stock (Davis Strait or Spitsbergen) were later killed or found dead in the waters inhabited by the other stock (Eschricht and Reinhardt, 1866; Reeves et al., 1983). In times when these whales were more plentiful, such overlap in ranges may have occurred; however, it is more likely that the present population in the eastern North Atlantic is a remnant of the severely depleted Spitsbergen stock (Reeves and Leatherwood, 1985; McQuaid, 1986; Moore and Reeves, 1993).

Possibly numbering only "in the tens" now (Christensen et al.[3]), this group of animals is thought to originally have been the most populous of the bowhead whale stocks (Braham, 1984; Woodby and Botkin, 1993). The majority of islands within this region were uninhabited, and it is likely that this stock rarely experienced human predation prior to commercial whaling (Ross, 1993). From 1660 to 1912, about 90,000 bowhead whales were harvested by commercial whalers, a total that does not include mortally wounded whales that escaped, whales captured but cast adrift, or cargos of vessels that were lost or captured at sea (Ross, 1993). Woodby and Botkin (1993) reevaluated the historical harvest data and developed a minimum preexploitation estimate of about 24,000 whales (an earlier estimate

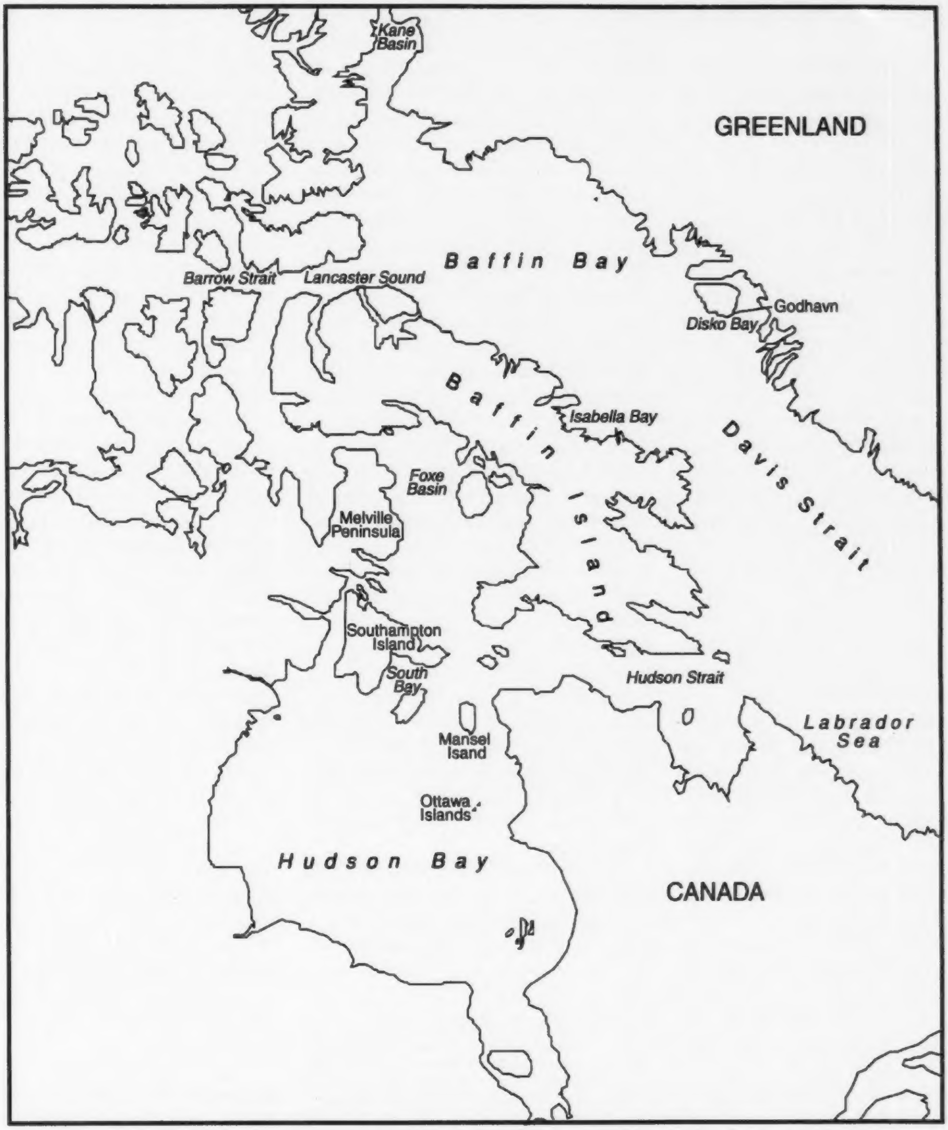


Figure 4. — Northeast Canada and Greenland with place names mentioned in the text (adapted from Moore and Reeves, 1993).

by Mitchell[4] came to 25,000). A maximum estimate was not computed because catch and voyage data (covering over 200 years of whaling) have not been fully compiled and analyzed (Ross, 1993; Woodby and Bodkin, 1993).

Davis Strait Stock

Bowhead whales in the western North Atlantic are currently segregated into two stocks, one occupying Davis Strait, Baffin Bay, and along the Canadian Arctic Archipelago (Davis Strait stock) and the other found in Hudson Strait, Hudson Bay, and Foxe Basin (Hudson Bay stock) (as defined in Moore and Reeves, 1993; Fig. 4). This distinction is uncertain given that it is not based on genetic or morphological evidence; instead the two are separated based on their summer feeding distri-

[4] Mitchell, E. D. 1977. Initial population size of bowhead whale (*Balaena mysticetus*) stocks: cumulative catch estimates. Int. Whal. Comm. Unpubl. Doc. SC/29/33, 113 p.

butions (Reeves et al., 1983; Reeves and Mitchell, 1990).

The Davis Strait stock is believed to follow a counterclockwise migration pattern similar to the Spitsbergen stock (Ross, 1993). Animals move northeast from the Labrador Sea across Davis Strait to the west coast of Greenland, following the pack ice as it recedes. Some cross Baffin Bay to Lancaster Sound, the summer feeding grounds north of Baffin Island, while others continue north along the Greenland coast to Kane Basin or west of Baffin Island into Barrow Strait (Davis and Koski, 1980; Reeves et al., 1983). Some exchange between the eastern North Atlantic stocks and the Bering Sea stock has been documented (based on whaling irons used in the Davis Strait fishery that were found in whales taken in the Chukchi Sea) (Bockstoce and Burns, 1993). Segregation by size and sex appears to occur at this time: cows with calves and subadults are found around the inlets and islands north and west of Baffin Island while other adults occupy the waters along the northeast coastline (Reeves et al., 1983; Reeves and Mitchell[5]). The summer resident population of Isabella Bay (east-central Baffin Island) has consisted predominantly of adults and large subadults (Finley, 1990; Richardson et al., 1995). Early whalers believed this segregation continued through the southbound migration (Southwell, 1898). Cows, calves, and young whales followed the east coastline of Baffin Island back to the Labrador Sea, while large adults ("old males") moved south along the western coast (Southwell, 1898, summarized in Ross, 1993). This may be true in part as calves and small juveniles (<10m in length) are rarely observed in Isabella Bay (Finley, 1990). Some whales may migrate south along the west coast of Greenland (Kapel, 1985) while others may overwinter in polynyas and flaw zones within the pack ice (Reeves et al., 1983; Turl, 1987; McLaren and Davis[6]; Richard et al.[7]). Unlike the Spitsbergen stock, whalers did not attribute variations in size and migration patterns to the existence of multiple stocks in Davis Strait (Reeves et al., 1983). The recent reidentification of a whale photographed in Isabella Bay in September 1986 and again near Disko Bay, West Greenland, on 10 April 1990 (Heide-Jørgensen and Finley, 1991) appears to support the hypothesis that these whales belong to one stock.

Recent research on the Davis Strait stock has focused on summer residents and southbound migrants utilizing Isabella Bay (Finley, 1990; Richardson et al., 1995). Additional sightings include the entanglement of a bowhead whale off northwest Greenland in early November 1980 (Kapel, 1985) and incidental sightings made during surveys for beluga whales, *Delphinapterus leucas*, and narwhals, *Monodon monoceros*, conducted off West Greenland in March 1990, 1993, 1994, and April 1991 (Reeves and Heide-Jørgensen[8]). Monitoring this population has proven to be difficult given its large range and severely reduced numbers (Finley, 1990; Reeves and Heide-Jørgensen[8]). Since 1980, no long-term studies have been made of this stock outside of Isabella Bay (Finley, 1990; Reeves and Heide-Jørgensen[8]).

Current estimates of Davis Strait stock abundance are based on sightings gathered by Davis and Koski (1980), Finley (1990), and Koski and Davis[9]. From counts obtained during the fall migration in 1978, Davis and Koski (1980) concluded that the population was "in the low hundreds at most." In 1979, an estimated 140 ± 33 bowhead whales were observed migrating through the 1978 study area, separate from another group observed summering in Isabella Bay (Koski and Davis[9]). Using the numbers gathered from aerial photo-identification surveys, Finley (1990) estimated "as many as" 107 individual bowhead whales were in the vicinity of Isabella Bay in late September 1986. To this number Finley added the Koski and Davis[9] estimate from 1979 to obtain a "conservative" estimate of 250 animals for the entire stock. Zeh et al. (1993) reanalyzed the Finley (1990) data using a mark-recapture method sampling only the best quality photo images from 1986 (77 photographs) and 1987 (21 photographs). They obtained an estimate of 214 ± 54 bowhead whales in Isabella Bay, to which they added the 1979 Koski and Davis[9] estimate, yielding a total abundance of about 350 bowhead whales in the Davis Strait stock. Because only well marked animals were used in the analysis, this estimate is considered to be "conservative" (Zeh et al., 1993). Given the low proportion of calves (2.2–3.6%) observed during these surveys, recovery from past whaling "has been, at best, exceedingly slow" (Davis and Koski, 1980), and viability of the population may be at risk (Finley, 1990). The Davis Strait stock has had no appreciable evidence of recovery since the period of commercial whaling, over 80 years ago (Reeves et al., 1983).

Almost 29,000 bowhead whales were harvested in Davis Strait between 1719 and the end of commercial whaling in 1915 (Ross, 1993) from an estimated original stock of over 11,700 (Woodby and Botkin, 1993). Between 1922 and 1975, only seven whales were taken or struck and lost by Canadian Eskimos (Mitchell and Reeves, 1982; Reeves and Heide-Jørgensen[8]), and after 1979, the Canadian government "explicitly banned the hunting of bowheads without a license" under the Federal Cetacean Protection Regulations (Reeves and Mitchell, 1990). Though bowhead whales

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[5] Reeves, R. R., and E. Mitchell. 1991. Summer segregation in the Davis Strait bowhead whale stock. Int. Whal. Comm. Unpubl. Doc. SC/43/PS28, 1 p.

[6] McLaren, P. L., and R. A. Davis. 1983. Distribution of wintering marine mammals off West Greenland and in southern Baffin Bay and northern Davis Strait, March 1982. Rep. for Arctic Pilot Proj., Calgary, Alberta, by LGL Ltd., 98 p.

[7] Richard, P., J. Orr, R. Dietz, and L. Dueck. 1993. Preliminary report on an aerial survey of belugas in the North Water, 21–26 March 1993. Work. pap. pres. to Joint Commiss. Conserv. Manage. Narwhals and Belugas. Sci. Work. Group, Copenhagen, 21–23 June.

[8] Reeves, R. R., and M. P. Heide-Jørgensen. 1994. Recent observations of bowhead whales off West Greenland. Int. Whal. Comm. Unpubl. Doc. SC/46/NA11, 9 p.

[9] Koski, W. R., and R. A. Davis. 1980. Studies of the late summer distribution and fall migration of marine mammals in NW Baffin Bay and E Lancaster Sound, 1979. Rep. from LGL Ltd. to Petro-Can. Explor. Inc., 214 p. Avail. from Pallister Resour. Manage. Ltd., Suite 105, 4116–64th Ave. S.E., Calgary, Alberta, Can. T2C 3B3.

are currently designated as endangered by the Committee on the Status of Endangered Wildlife in Canada (COSEWIC) (Campbell, 1990), a request to harvest one whale per year by the Inuit of the eastern Northwest Territories has been made under the Nunavut Final Land Claim Agreement (Indian and Northern Affairs Canada 1993, summarized in Reeves and Heide-Jørgensen[8]). In Autumn 1994, a bowhead whale was illegally harvested from the Davis Strait stock by a Canadian native (Marine Mammal Commission[10]).

Hudson Bay Stock

As mentioned in the preceding Davis Strait Stock section, there is currently no evidence to suggest that the Hudson Bay stock is discrete from it. However, separating these two populations based on their summer distributions allows for a conservative approach to managing each one (Reeves and Mitchell, 1990). From the middle of May until September, bowhead whales of the Hudson Bay stock are commonly observed near Southampton Island in northwestern Hudson Bay and along the northern tip of the Melville Peninsula in Foxe Basin (Moore and Reeves, 1993; Fig. 4). Scattered sightings also have occurred along the western coastline of Hudson Bay and near the Ottawa Islands and Mansel Island of eastern Hudson Bay (Reeves and Mitchell, 1990). Bowhead whales observed in Hudson Strait, which connects the Bay to the Labrador Sea, are believed to be migrants leaving the Hudson Bay area in the autumn or returning in the spring (Finley et al., 1982; Reeves and Mitchell, 1990). A portion of the population overwinters in the upper Bay in leads and polynyas formed near islands (Low, 1906; Ross, 1975; Reeves and Mitchell, 1987).

Sightings usually have been of small groups of bowhead whales, rarely exceeding two individuals (Reeves et al., 1983, Reeves and Mitchell, 1990). Fifteen whales (in groups of 1, 2, 3, 4, and 5) were observed in upper Foxe Basin on 20 August 1983 (Orr et al., 1986), and in July 1981, twelve whales were seen in South Bay, Southampton Island (Reeves and Mitchell, 1990). Approximately 23 different bowheads were identified by McLaren and Davis[11] during aerial surveys conducted over Hudson Strait in winter. No single survey has adequately covered the range of this stock, and therefore it is not possible to extrapolate these counts into a population estimate. A conservative estimate by Mitchell[4] placed the current population at 100 or less. Recent observations indicate that "at least a few tens of whales" from this stock continue to occupy a large portion of their former range (Reeves and Mitchell, 1990).

Prior to commercial whaling, this population consisted of about 580 whales (Mitchell[4] as modified by Woodby and Botkin, 1993). From 1860 to 1915, 565 whales were harvested by commercial whalers (Ross, 1993). Between 1919 and 1976, 28 bowhead whales were killed or struck and lost by native hunters in western Atlantic waters (Reeves et al., 1983; Reeves and Mitchell, 1990). Of these, 23 were from the Hudson Bay stock. Since 1980, other incidents of bowheads being fired upon have been reported (as cited in Reeves and Mitchell, 1990). There has been no appreciable recovery of this stock, in part attributed to occasional hunting by natives (Reeves and Heide-Jørgensen[8]) and predation by killer whales (see section on Natural Mortality) (Reeves et al., 1983; Reeves and Mitchell, 1990).

Okhotsk Sea Stock

There has been some difficulty in assessing the historical distribution and abundance of bowhead whales in the Okhotsk Sea. Right whales, *Eubalaena glacialis*, and gray whales, *Eschrichtius robustus*, were sometimes misidentified as bowhead whales, and whaling records maintained during the short period of time this stock was hunted were incomplete (Bockstoce and Botkin, 1983). Whales in this stock were discovered by commercial whalers in 1848 (Bockstoce, 1986), but intensive hunting did not begin until 1852 when whales in the Bering Sea stock were no longer as plentiful in "traditional" whaling areas (Bockstoce and Burns, 1993). By 1860, the Okhotsk Sea stock was severely depleted, and whalers had already resumed whaling in the Bering Sea (Bockstoce, 1986). Mitchell[4] estimated the preexploitation size of the population to be 6,500 based on a total estimated catch of 3,506 whales. Ross (1993) suggested that this estimate may be too high for the reasons stated above and offered "a conservative, though mostly speculative, compromise" of 3,000 as a minimum population estimate.

Though Scammon (1874) stated that bowheads were hunted "throughout the whole extent" of the Okhotsk Sea, certain areas were occupied by concentrations of animals during the summer months (Fig. 5). In the northeastern Okhotsk Sea, whales were found in Penzhinskaya Gulf and Gizhiginskaya Gulf. The next area of concentration was to the southwest in Tauyskaya Bay. Farther south, the best whaling grounds were within the gulfs and bays south of the Shantarskiye Islands and west of Sakhalin Island; Moore and Reeves (1993) provide additional details. Almost all of the areas where summer concentrations of bowhead whales occurred in the past are still occupied today (Table 1). As recent as August 1995, during joint Russian–American surveys, a few dozen bowhead whales were observed in a feeding aggregation south of the Shantarskiye Islands (Brownell[12]). Berzin et al. (1990) estimated the population in this area to be at least 250–300 animals. An estimate of abundance of 300–400 was made for the entire Okhotsk Sea based on data collected since 1979 (Vladimirov, 1994:Table 1). However, "no quantitative data are available to confirm" these estimates

[10] Marine Mammal Commission. 1995. Annual report to Congress, 1994. Mar. Mamm. Comm., 1825 Conn. Ave. N.W., Wash., D.C. 20009, 270 p.

[11] McLaren, P. L., and R. A. Davis. 1982. Winter distribution of Arctic marine mammals in ice-covered waters of eastern North America. Rep. for Petro-Can. Explor. Inc., Calgary, Alberta, by LGL Ltd. Offshore Labrador Biol. Stud. (OLABS) program rep., 151 p. Avail. from Pallister Resour. Manage. Ltd., Suite 105, 4116–64th Ave. S.E., Calgary, Alberta, Can. T2C 3B3.

[12] Brownell, R. L. NMFS, Southwest Fisheries Science Center, La Jolla, CA, 92038. Personal commun.

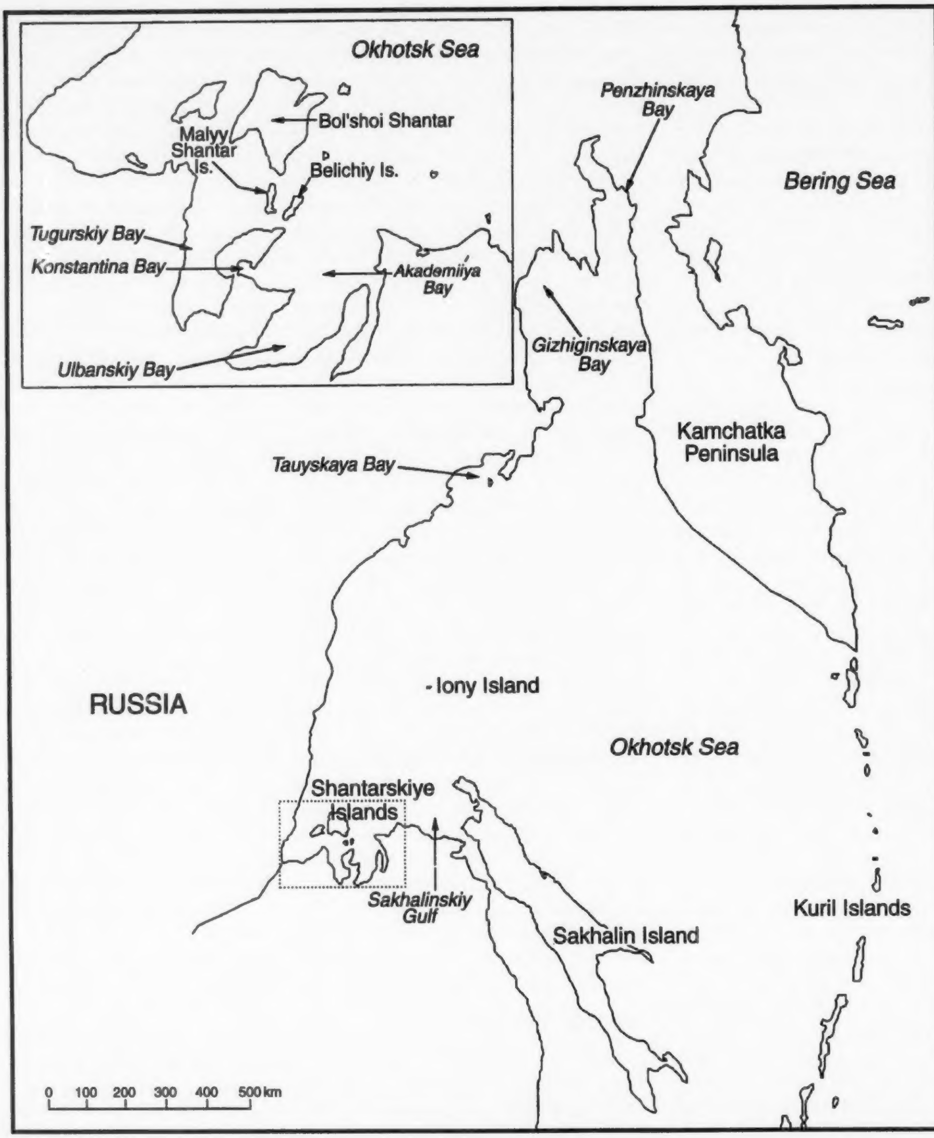


Figure 5. — Okhotsk Sea and environs with place names mentioned in the text (adapted from Moore and Reeves, 1993).

(Berzin et al.[13]). There is some speculation as to whether animals found during the summer in the northeastern Okhotsk Sea form a distinct population from those in the Shantarskiye region. The winter distribution of both of these groups is unknown.

Berzin et al. (1991) noted that by mid-November, bowhead whales were no longer found in the Shantarskiye region, despite the waters being ice-free. Fedoseev (1984) observed bowhead whales deep in the ice north of Sakhalin Island in 1969, 1981, and 1983, in addition to one sighting east of Sakhalin Island in 1981 and another a little over 200 km south of Tauyskaya Bay in 1982 (Table 2). Because whalers left the Okhotsk Sea before the onset of winter storms in early November and did not

[13] Berzin, A. A., S. A. Blokhin, H. Minakuchi, R. L. Brownell, A. M. Burdin, and V. N. Burkanov. 1995. Bowhead and gray whale populations in the Okhotsk Sea. *In* Abstracts of the North Pacific Marine Science Organization (PICES): workshop on the Okhotsk Sea and adjacent areas, Vladivostok, Russia, 19–24 June 1995, p. 44–45.

Table 1.—Recent sightings of bowhead whales in historic summer concentration areas in the Okhotsk Sea. Commas separate sightings that were made at different times (days or months) during the survey year.

General location of sightings	1982[1]	1983[1]	1984[1]	1986[2,3]	1987[2,4]	1988[2]	1989[5]	1990[5]
N.E. Okhotsk Sea								
Penzhinskaya Gulf	U[6]	U	U	U	U	2	U	U
Gizhiginskaya Gulf	U	U	U	17	U	7	19, 36	U
S.W. Okhotsk Sea								
Between Bol'shoi Shantar Island and Utichiy Island	U	U	U	18	U	U	8, 14, 21, 33	U
Tugurskiy Bay	U	3	U	U	U	U	U	1
Konstantina Bay	13	2	20	U	47	72	U	44, 7+20
Ulbanskiy Bay	15	U	11	U	40	>30	72[7], 1's	
Akademiya Bay	U	39	U	U	U	U	U	

[1] Data from Berzin et al. (text footnote 39). Surveys occurred during 1–7 September 1982, 30 August–7 September 1983, and 21–23 August, 20 October 1984.
[2] Data from Berzin et al. (1990). The 1986 sighting occurred in early June (N.E. Okhotsk Sea); the 1987 sighting was in July; the 1988 sightings occurred in late May (N.E. Okhotsk Sea), on 7 August (Konstantina Bay, including 2 calves), and on 20 October (Ulbanskiy Bay).
[3] Data from IWC (1988:113). The 1986 sighting occurred in September (S.W. Okhotsk Sea).
[4] Data from Berzin et al. (1988). The 1987 sighting occurred in October (Ulbanskiy Bay).
[5] Data from Berzin et al. (1991). The 1989 sightings occurred on 23 May (19), 24 May (36 including 2 calves), May 28 (8), the morning of 31 May (14), the afternoon of 31 May (21), 1 June (33), late August (72), and 28–30 September ("singly and far apart"). The 1990 sightings occurred on 24–25 June (1), 27 August (44 around the cape separating Konstantina and Ulbanskiy Bay), and 28 August (7 near the cape, 20 spread througn Ulbanskiy and Akademiya Bay).
[6] U = unknown whether the area was surveyed or not.
[7] This sighting is incorrectly attributed to the 1989 season in Berzin et al. (1991); the sighting occurred during the 1988 season only (Brownell, text footnote 12).

Table 2.—Bowhead whales observed outside of summer concentration areas in the Okhotsk Sea (from Fedoseev, 1984).

Date	Location	Lat.	Long.	Group size
8 Apr. 1969	N. of Sakhalin Island	55°10'N	144°30E	6
11 Apr. 1981	"	55°20'N	144°15E	23
		55°15'N	144°00E	2
7 May 1981	"	56°00'N	141°20E	8+7
9 May 1981	"	54°58'N	143°15E	7
21 Dec. 1983	"	57°30'N	143°00E	2
1981[1]	E. of Sakhalin Island	Not noted in text		3
29 Dec. 1982	S. of Tauyskaya Bay	56°22'N	150°00E	4

[1] Sighting was noted on Figure 1 (Fedoseev, 1984) but not described within the text.

return until June, there are no historic records on bowhead whale distribution during this whaling hiatus, leaving the possibility that there originally was a common stock between the Okhotsk and Bering Seas (Townsend, 1935). However, other authors (Bockstoce and Botkin, 1983; Lindholm[14]) have argued that the Okhotsk Sea stock has always been a population discrete from the Bering Sea stock.

Bering Sea Stock

The Bering Sea stock, also referred to as the western Arctic stock or the Bering-Chukchi-Beaufort stock, has been studied more extensively than any of the aforementioned stocks. This stock is widely distributed in the central and western Bering Sea in winter (November to April), generally associated with the marginal ice front, and found near the polynyas of St. Matthew and St. Lawrence Islands and the Gulf of Anadyr (Bogoslovskaya et al., 1982; Brueggeman, 1982; Braham et al., 1984; Ljungblad et al.[15]; Brueggeman et al.[16]; Bessonov et al.[17]; Fig. 6). From April through June, these whales migrate north and east, following leads in the sea ice in the eastern Chukchi Sea until they pass Point Barrow where they travel east toward the southeastern Beaufort Sea (Braham et al., 1980; Braham et al., 1984; Marko and Fraker[18]). Most of the summer (June through September), bowhead whales range through the Beaufort Sea (Hazard and Cubbage, 1982; Richardson et al., 1987; McLaren and Richardson[19]; Richardson et al.[20]; Richardson et al.[21]). Spatial distribution seems to vary between years (Richardson et al., 1987; Davis et al.[22]; Thomson et al.[23]) affected in part by surface temperature or turbidity fronts and anomalies (Borstad, 1985; Thomson et al.[23]).

Very few bowhead whales are found in the Chukchi Sea in summer (Miller et al., 1986); however, there have been enough sightings to indicate that some whales do not migrate to the Beaufort Sea, at least during some years. Many small groups have been observed traveling northwest along the Chukchi Peninsula in May (Bogoslovskaya et al.,

[14] Lindholm, O. 1863. Whales and how tides and currents in the Okhotsk Sea affect them. [From an unidentified journal with news from the Far East of Russia, p. 42–43. In Russ. Transl. by L. A. Hutchinson for Univ. Calif. San Diego, La Jolla, 1965, 12 p.]

[15] Ljungblad, D. K., S. E. Moore, J. T. Clarke, and J. C. Bennett. 1986. Aerial surveys of endangered whales in the northern Bering, eastern Chukchi and Alaskan Beaufort Sea, 1985: with a seven year review, 1979–85. Rep. for U.S. Minerals Manage. Serv. by Nav. Ocean Systems Cent., NTIS No. PB87-115929, 443 p.

[16] Brueggeman, J. J., B. Webster, R. Grotefendt, and D. Chapman. 1987. Monitoring the winter presence of bowhead whales in the Navarin Basin through association with sea ice. Rep. for U.S. Minerals Manage. Serv. by Envirosphere Co., NTIS No. PB88-101258, 179 p.

[17] Bessonov, B., V. V. Mel'nikov and V. A. Bobkov. 1990. Distribution and migration of cetaceans in the Soviet Chukchi Sea. *In* Conference Proceedings, Third Information Transfer Meeting, p. 25–31. U.S. Minerals Manage. Serv., Alaska OCS Reg.

[18] Marko, J. R., and M. A. Fraker. 1981. Spring ice conditions in the Beaufort Sea in relation to bowhead whale migration. Rep. for Alaska Oil Gas Assoc., Anchorage, by LGL Ltd., 98 p.

[19] McLaren, P. L., and W. J. Richardson. 1985. Use of the eastern Alaskan Beaufort Sea by bowheads in late summer and autumn. *In* LGL and Arctic Science, Importance of the eastern Alaskan Beaufort Sea to feeding bowheads: literature review and analysis, p. 7–35. Rep. for U.S. Minerals Manage. Serv. by LGL, Inc., and Arctic Sci., Ltd., 158 p.

[20] Richardson, W. J., B. Würsig, G. W. Miller, and G. Silber. 1986. Bowhead distribution, numbers and activities. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985, p. 146–219. Rep. for U.S. Minerals Manage. Serv. by LGL Inc., OCS Study MMS 86-0026. NTIS No. PB87-124350, 315 p.

[21] Richardson, W. J., B. Würsig, and G. W. Miller. 1987. Bowhead distribution, numbers and activities. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985–86, p. 257–368. Rep. for U.S. Minerals Manage. Serv. by LGL Inc., NTIS No. PB88-150271, 547 p.

[22] Davis, R. A., W. R. Koski, and G. W. Miller. 1983. Prelimary assessment of the length-frequency distribution and gross annual recruitment rate of the western arctic bowhead whale as determined with low-level aerial photogrammetry, with comments on life history. Rep. to NMFS, Natl. Mar. Mamm. Lab., Seattle, Wash., by LGL Ltd., 91 p.

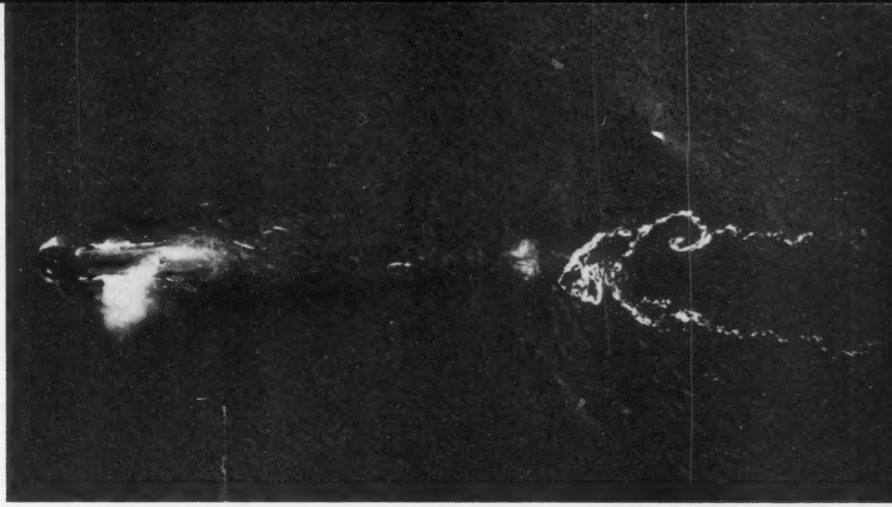
[23] Thomson, D. H., D. B. Fissel, J. R. Marko, R. A. Davis, and G. A. Borstad. 1986. Distribution of bowhead whales in relation to hydrometeorological events in the Beaufort Sea. Environ. Stud. Revolving Funds Rep. 028, 119 p. Can. Dep. Indian N. Affairs, Ottawa.

Figure 6. — Bering Sea and environs with place names mentioned in the text.

1982; Bessonov et al.[17]; Ainana et al.[24]; Zelensky et al.[25]), and about 60 whales traveled northwest past Cape Serdtse-Kamen 15–28 June 1990 (Mel'nikov and Bobkov, 1993). One group of 7 whales was observed off Cape Netten, Chukchi Peninsula, on 26 July 1991 traveling north, and a group of 7 was seen here on 27 September traveling east (Mel'nikov and Bobkov, 1994). Farther northwest, near Cape Schmidt, single animals were observed on 5 Au-

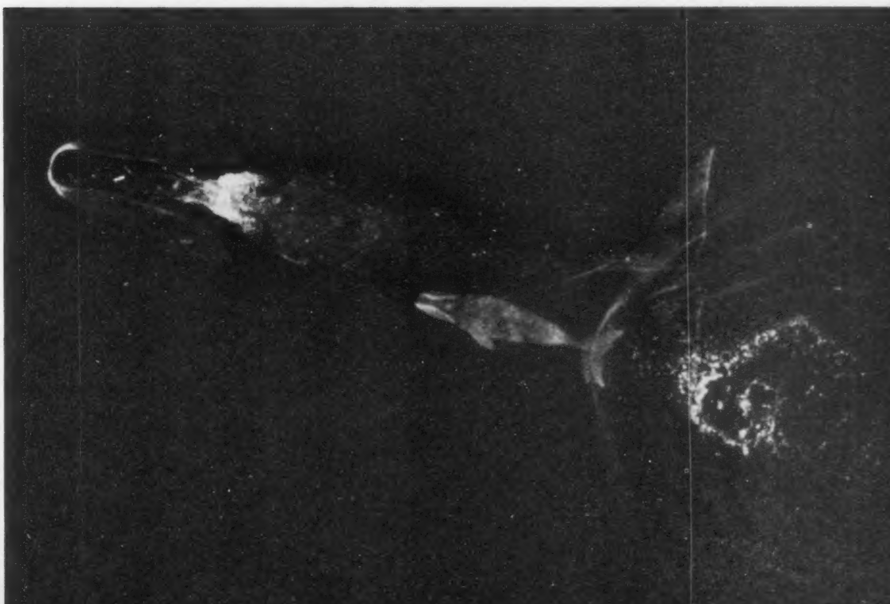
[24] Ainana, L., N. Mymrin, L. Bogoslovskaya, and I. Zagrebin. 1995. Role of the Eskimo Society of Chukotka in encouraging traditional Native use of wildlife resources by Chukotka Natives and in conducting shore based observations on the distribution of bowhead whales, *Balaena mysticetus*, in coastal waters off the south-eastern part of the Chukotka Peninsula (Russia) during 1994. Rep. to Dep. Wildl. Manage., North Slope Borough, Barrow, Alaska, by Eskimo Soc. Chukotka, Provideniya, Russia, 135 p.

[25] Zelensky, M., V. V. Mel'nikov, and V. V. Bichkov. 1995. Role of the Naukan Native Company in encouraging traditional Native use of wildlife resources by Chukotka Native people and in conducting shore based observations on the distribution of bowhead whales, *Balaena mysticetus*, in waters of the Bering Sea and Chukchi Sea adjacent to the Chukotka Peninsula (Russia) during 1994. Rep. to Dep. Wildl. Manage., North Slope Borough, Barrow, Alaska, by Eskimo Soc. Chukotka, Provideniya, Russia, 105 p.



Aerial view of a bowhead whale migrating past Point Barrow, Alaska, during the 1992 spring migration. A column of vapor, the "blow," exits the open blowholes. White on the chin and tail are characteristic of bowheads, and acquired marks along the dorsal surface allow for reidentification of this individual if photographed again. Photo by Wayne Perryman, NMFS.

A bowhead whale feeds in the Beaufort Sea (swimming to the left in this image). The high blowhole, "neck," and broad back are characteristic of this species. Photo by David Rugh, NMFS.



Aerial view of a bowhead whale adult and calf migrating past Point Barrow, Alaska, during the 1992 spring migration. The calf is in the typical swimming position beside the adult and between the pectoral flipper and fluke. Photo by Robin Westlake, NMFS.

gust and 1 September by crew members of the ice-breaker *Krasin*. Studies conducted in 1994 have shown the presence of bowhead whales throughout the summer along the southeastern portion of the Chukchi Peninsula (127 sightings in June, 59 in July, 5 in August, and 6 in September (Ainana et al.[24])) and the easternmost portion of the Peninsula (21 sightings in June and 39 in August (Zelensky et al.[25])).

During late summer (early September to mid-October), bowhead whales migrate west out of the Beaufort Sea, as evidenced during aerial surveys (Richardson [26]; Ljungblad et al.[27]), radio-tracking (Wartzok et al.[28]), and satellite- tracking (Mate and Krutzikowsky[29]). From mid-September to mid-October they are seen in the northeast Chukchi Sea, some as far north as lat. 72°N (Moore et al., 1986; Moore and Clark[30]). Whales migrate from Point Barrow into the Chukchi Sea heading toward Wrangel Island (Mate and Krutzikowsky[29]). When they reach the Siberian coast, they follow it southeast to the Bering Strait (Bogoslovskaya et al., 1982; Zelensky et al.[25]). In 1991, fall migrants, presumably returning from the Beaufort Sea, did not begin passing Cape Netten until 10 November (Mel'nikov and Bobkov, 1994). By early winter (late October and November) they arrive in the Bering Sea (Kibal'chich et al., 1986; Bessonov et al.[17]), where they remain until the following spring migration.

Segregation by size and sex class occurs in three overlapping pulses during the spring migration, the first consisting of subadults, the second of larger whales, and the third composed of even larger whales and cows with calves (Rugh, 1990; Angliss et al., 1995; Nerini et al.[31]). The reverse appears to occur along the Chukchi Peninsula; Russian natives noted the appearance of large numbers of mothers with calves in late March and early April followed by immature and adult animals (Bogoslovskaya et al., 1982). In the Beaufort Sea in summer, aggregations have usually consisted of only juveniles or of large whales that may include calves (Richardson[26], Davis et al.[32]). In 1983, Cubbage and Calambokidis (1987) found a significant inverse correlation between longitude and size class; encounter rates for larger whales increased moving west to east in the Beaufort Sea. Onshore and offshore distributions varied annually, suggesting that "sex- or age-class segregation patterns are temporally and spatially fluid and cannot be defined rigidly for any region or period" (Moore and Reeves, 1993:351). Segregation by size also occurs during the fall migration (Braham, 1995). George et al. (1995) showed a clear trend in progressively smaller whales harvested between August and November. Along the Chukchi Peninsula, the fall migration splits into two pulses (Bogoslovskaya et al., 1982; Mel'nikov and Bobkov, 1993; 1994), though segregation by size or sex class was not confirmed as the cause.

The sex ratio of whales harvested by Alaska natives from 1973 to 1992 was equal, though the proportion of adult females harvested in the spring has increased from 4.7% (1973–77) to 20.4% (1986–92) (Braham, 1995). Immature whales (<13 m) made up the largest percentage of the harvest; 80% prior to 1978 and 60% since 1978 (Braham, 1995). Records from the historical commercial catch were not as well maintained. Unlike the commercial whalers in the North Atlantic region, whalers in the North Pacific sector did not document size or sex differences between the aggregations of animals they hunted (Bockstoce and Burns, 1993).

Whales taken by commercial whalers in the Bering Sea may have been representatives of a population that did not migrate (Bockstoce and Botkin, 1983; Bockstoce, 1986; Fraker[33]). After reducing the number of bowhead whales in the Bering Sea to a point where they were uneconomical to hunt, the whalers turned their attention to the Okhotsk Sea. And when the Okhotsk Sea stock was nearly eliminated, the whalers explored the Chukchi Sea. Because they did not find whales in the western Chukchi Sea, they continued east to the Beaufort Sea where large numbers were found (Bockstoce and Burns, 1993). There has been difficulty in assessing the total number of animals killed in the Bering Sea stock. Only 19% of commercial whaling records collected from 1849 to 1914 have been extensively analyzed (Bockstoce and Botkin, 1983). Woodby and Botkin (1993) reviewed the summaries of estimated annual kills from pelagic and shore-based fisheries compiled by Marquette and Bockstoce (1980), Bogoslovskaya et al. (1982), Bockstoce and Botkin (1983), Breiwick and Mitchell (1983), Breiwick et al. (1984), Sonntag and Broadhead (1989), Mitchell[4], and Braund et al.[34]. They created a time series of harvest data showing cumulative kill records for each year

[26] Richardson, W. J. (Editor). 1987. Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales, 1985–86. Rep. for U.S. Minerals Manage. Serv. by LGL Inc., NTIS No. PB88-150271, 547 p.

[27] Ljungblad, D. K., S. E. Moore, J. T. Clarke, and J. C. Bennett. 1987. Distribution, abundance, behavior and bioacoustics of endangered whales in the Alaskan Beaufort and eastern Chukchi Seas, 1979–86. Rep. for U.S. Minerals Manage. Serv. by Nav. Ocean Systems Cent., NTIS No.AD-A183934/9, 391 p.

[28] Wartzok, D., W. A. Watkins, B. Würsig, J. Guerrero, and J. Schoenherr. 1990. Movements and behaviors of bowhead whales. Rep. from Purdue Univ., Fort Wayne, for AMOCO Prod. Co., Anchorage, 197 p.

[29] Mate, B. R., and G. Krutzikowsky. 1995. Application of remote methods of large cetacean tracking: bowhead whales. Rep. for U.S. Minerals Manage. Serv. by Hatfield Mar. Sci. Cent., Oregon State Univ., Newport. OCS Study MMS 95-0053, 174 p.

[30] Moore, S. E., and J. T. Clarke. 1992. Distribution, abundance and behavior of endangered whales in the Alaskan Chukchi and western Beaufort Seas, 1991: with a review 1982–91. Rep. for U.S. Minerals Manage. Serv., Anchorage, Alaska, by SAIC, Marit. Serv. Div., 237 p.

[31] Nerini, M. K., D. Withrow, and K. Strickland. 1987. Length structure of the bowhead whale population derived from aerial photogrammetry, with notes on recruitment spring 1985 and 1986. Int. Whal. Comm. Unpubl. Doc. SC/39/PS14, 22 p.

[32] Davis, R. A., W. R. Koski, G. W. Miller, P. L. McLaren, and C. R. Evans. 1986. Reproduction in the bowhead whale, summer 1985. Int. Whal. Comm. Unpubl. Doc. SC/38/PS2, 123 p.

[33] Fraker, M. A. 1984. A brief review of recent information on the responses of bowhead whales (*Balaena mysticetus*) to offshore petroleum operations. Int. Whal. Comm. Unpubl. Doc. SC/36/PS17, 19 p.

[34] Braund, S. R., W. M. Marquette, and J. R. Bockstoce. 1988. Data on shore-based bowhead whaling at sites in Alaska. Int. Whal. Comm. Unpubl. Doc. SC/40/PS10, 9 p.

from 1848 to 1991. According to these data, 22,174 bowhead whales have been harvested from a stock that may have numbered between 10,000 and 23,000 before commercial exploitation. From 1992 to 1994, 113 bowhead whales were landed and 35 were struck but lost during native subsistence hunts in Alaska (Suydam et al., 1995).

Several different methods have been used to compute the current population size of the Bering Sea stock (reviewed by Zeh et al., 1993). In 1994, the International Whaling Commission's (IWC) Scientific Committee reviewed data collected during the 1993 visual and acoustic census (Zeh et al., 1995; Raftery and Zeh[35]) conducted near Point Barrow. They settled on a current population estimate of 7,992 bowhead whales (95% C.I.: 6,900–9,200) (IWC, 1995; Marine Mammal Commission[10]). Zeh et al.[36] continued to refine their estimate using newly available acoustic data. The 1988 Bayes empirical Bayes method yielded a population estimate of 7,500 (95% C.I.: 6,400–9,200). An alternative method, the N_4/P_4 method, which compared the estimated number of whales passing within the viewing range of census observers (N_4) and the proportion detected by the hydrophone array (P_4), resulted in an estimate of 8,000 (95% C.I.: 6,900–9,200) for the 1993 census. The Bayes empirical Bayes method "provided the best information on population size for assessment purposes" while the N_4/P_4 method provided "the best available estimate of the current size" of the Bering Sea stock (IWC, 1995; Zeh et al.[36]). An annual rate of increase of 3.1% (95% C.I.: 1.4–4.7%) was computed for the Bering Sea stock (IWC, 1995; Zeh et al.[36]).

A quota of 204 bowhead whales has been set for 1995–98 (see section on Management), based on a stated need for 51 whales per year to be divided among ten Alaskan native villages (IWC, 1995; Marine Mammal Commission[10], Zeh et al.[36]). Requests to harvest bowhead whales have also been put forth by Canadian and Russian natives. In 1991, Aklavik hunters in the western Canadian Arctic requested a permit to kill one or strike two bowhead whales from the Bering Sea stock (Freeman et al., 1992). Permission was granted by the Canadian government in August 1991, and one whale was harvested in Mackenzie Bay in the autumn of 1991 (Stoker and Krupnik, 1993; Marine Mammal Commission[10], Zeh et al.[36]). Additional licenses were granted in 1993 and 1994, though bowhead whales were not harvested in either year (Marine Mammal Commission[10], Zeh et al.[36]). Aboriginal harvests along the Chukchi Sea coasts usually yielded 8–10 bowhead whales in "good years" in the early 20th century, but by the mid-20th century, bowhead whale hunting was almost completely replaced by gray whale hunting (Krupnik, 1987). Poverty in the villages along the Chukchi Sea coast has brought about a renewed interest in hunting one or two bowhead whales a year (Bogoslovskaya et al., 1982; Bessonov et al.[17]).

Life History and Ecology

Most of what is known of the life history and ecology of bowhead whales has been derived from studies of the Bering Sea stock. The data presented in this section applies only to this stock unless otherwise stated.

Feeding

Food habits studies conducted on 35 bowhead whales (21 males and 14 females) harvested between 1975 and 1989 by Alaskan natives were reviewed by Lowry (1993). Most prey species identified from bowhead whale stomach contents were crustacean zooplankton, particularly euphausiids and copepods ranging in length from 3 to 30 mm. Epibenthic organisms, mostly mysids and gammarid amphipods, were also common in stomach contents, with only a small sampling of benthic species (Lowry, 1993). Age-related differences were difficult to establish given the limited sample size; however, slightly higher levels of epibenthic organisms were found in the stomachs of small whales (<10.5 m in length) (Lowry, 1993), and it appears that copepods become increasingly more important in the diet of larger whales (Schell et al.[37]). Crustacean zooplankton was the dominant prey in both males (89%) and females (79%) (Lowry, 1993).

As evidenced in stomach contents collected between April and June, some bowhead whales feed opportunistically during the spring migration (George and Tarpley, 1986; Carroll et al., 1987; Lowry, 1993). In most cases, half or more of the stomachs were empty (3 of 6 near St. Lawrence Island, 3 of 4 at Point Hope, 10 of 12 at Wainwright, and 23 of 36 near Point Barrow). Stomachs collected south of Point Barrow were from small whales and contained "shrimp," gammarid amphipods or very small (<3.1 mm) copepods. Stomachs collected from whales collected near Point Barrow generally contained either copepods, euphausiids, or both, though the dominant prey often varied between individuals harvested in the same year. During the fall migration, only 2 of 15 whales harvested off Kaktovik (central Beaufort Sea) and 1 of 6 taken near Barrow had empty stomachs (Lowry, 1993). Sex- and length-related differences in diet were not noted in the 11 samples collected at Kaktovik (4 females and 7 males) that underwent detailed examination. Copepods were predominant in six of the stomach samples, euphausiids in three, mysids in one, and one contained almost equal parts of all three organisms. Euphausiids were the dominant prey item found in five large whales (>14 m) harvested near Point Barrow in September.

In years when oceanographic conditions are favorable, the lead system near Point Barrow may serve as an important feeding ground in the spring

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[35] Raftery, A. E., and J. E. Zeh. 1994. Bowhead whale, *Balaena mysticetus*, population size estimated from acoustic and visual census data collected near Barrow, Alaska, in 1993. Int. Whal. Comm. Unpubl. Doc. SC/46/AS13, 25 p.

[36] Zeh, J. E., A. E. Raftery, and A. A. Shaffner. 1995. Revised estimates of bowhead population size and rate of increase. Int. Whal. Comm. Unpubl. Doc. SC/47/AS10, 26 p.

[37] Schell, D. M., S. M. Saupe, and N. Haubenstock. 1987. Bowhead whale feeding: allocation of regional habitat importance based on stable isotope abundances. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales 1985–86, p. 369–415. Rep. to U.S. Minerals Manage. Serv. by LGL Ecol. Res. Assoc. Inc., NTIS No. PB88-150271.

(Carroll et al., 1987). Other important feeding grounds exist in the Beaufort Sea (Lowry and Frost, 1984; Ljungblad et al., 1986; Schell and Saupe, 1993; Würsig et al., 1985; 1989; Thomson and Richardson[38]), along the northern Chukchi Peninsula (Mel'nikov and Bobkov, 1993; 1994; Moore et al., 1995) and possibly in the Bering Sea (Schell and Saupe, 1993). Schell and Saupe (1993) and Schell et al.[37] believe that a significant amount of feeding may occur outside the eastern Beaufort Sea, particularly by older whales in the fall and early winter when they are in the Chukchi and Bering Seas. These conclusions are based on patterns of isotope variation found in the visceral fat and muscle sampled from three adults and six subadults. This variability suggests that older animals are feeding in different areas or on different prey types than younger animals. Feeding behavior has been observed during the summer in the Beaufort Sea and the fall in the Chukchi Sea but not in the winter in the Bering Sea, as summarized by Lowry (1993).

The occupation of summer concentration areas by bowhead whales in the Okhotsk Sea is believed to be influenced by distributions of prey (Berzin et al.[39]), though feeding aggregations were only reported in 1979 and 1995 (Brownell[12], Berzin et al.[39]). In the Davis Strait stock, feeding behavior was observed in bowhead whales summering in Isabella Bay, Baffin Island (Finley, 1990). Most of this activity took place in deep (>200 m), glacial troughs where large concentrations of *Calanus* copepods occurred (Finley, 1990; Nicklin, 1995; Richardson et al., 1995). Information on food habits of the Spitsbergen stock is sparce. Scoresby (1820) found Greenland whale stomachs contained predominantly small crustaceans he called "squillae and shrimps." Scoresby's drawings were examined by Ruud (1937) who determined that the "squillae" were partially digested euphausiids.

Reproduction

Although apparent sexual activity occurs among bowhead whales most months of the year, studies of bowhead fetuses indicate conception typically occurs during late winter or early spring, as summarized by Koski et al. (1993:249). Not all sexual activity leads to conception; fecundity of some bowheads is in doubt with the discovery of pseudohermaphroditism in at least two males with testicular feminization (Tarpley et al.[40]), a relatively high incidence rate as only 76 bowheads have been closely examined between 1980 and 1989 (Philo et al., 1993). Calves are usually born between April and early June during the spring migration (Koski et al., 1993) probably peaking in May (Nerini et al., 1984). Most (76%) photogrammetrically measured calves were within 1 m of their average length in late spring (4.25–5.25 m) indicating a majority are born within a restricted period (Koski et al., 1993). Pregnancy rates have been documented as 0.21 pregnancies/mature female/year (Tarpley et al.[41], which includes results from Nerini et al., 1984) or 0.20–0.35 (George et al., 1995) with a possible increase in pregnancy rates of whales harvested since 1985 (George et al., 1992). These pregnancy rates suggest that mature female bowheads have calving intervals of 3.5–7.1 years (Nerini et al., 1984) or 4 years (Tarpley et al.[41]), comparable to calving intervals of right whales (Kraus et al., 1986; Bannister, 1990; Best, 1990; Hamilton and Mayo, 1990; Payne et al., 1990). The 3–4 year calving interval in bowhead whales has been corroborated by photo-identification evidence (Miller et al., 1992; Rugh et al., 1992). The highest sighting rate of calves during the spring migration occurred in 1993. This sighting rate, when graphed with earlier shore-based census and aerial photogrammetric sightings, provides additional support for a 3–4 year variable recruitment pattern (George et al., 1995).

Gestation lasts 13–14 months (Nerini et al., 1984) or 12–16 months (Tarpley et al.[41]). Calves are 4.0–4.5 m in length when born and increase from modal lengths of 4.75–5.0 m in late May to 6.25–6.5 m in late summer, a growth rate of 1.5 cm/day (Koski et al., 1993), much less than the 2.88 cm/day calculated for southern right whales (Best and Rüther[42]). Weaning occurs 9–15 months postpartum (Nerini et al., 1984) with about 95% of the yearlings weaned by the next spring migration (Rugh et al., 1992). Yearlings are 6.6–9.4 m long in the spring according to data from harvested whales (Nerini et al., 1984) and 7.0–8.7 m in summer based on photogrammetric lengths (Koski et al., 1993). Growth rates appear to slow after weaning. Small bowheads reidentified between years had growth rates of much less than 1 m/yr (Koski et al., 1992; Davis et al.[32]). Carbon isotope analysis, using apparent oscillations in isotopic ratios in tissue samples from baleen to indicate annual cycles, also suggests bowhead whales grow slowly, taking on the order of two decades to reach sexual maturity (Schell et al., 1989; Schell and Saupe, 1993). This growth rate is much slower than that of other baleen whales (Lockyer, 1981; 1990; Payne et al., 1990). Conventional techniques to age bowhead whales have been considered unsuccessful (Nerini[43]), in part because of the poor correlation between whale size and indicated age, but some evidence, such as ivory or stone harpoon heads found in five recently

[38] Thomson, D. H., and W. J. Richardson. 1987. Integration. *In* W. J. Richardson (Editor), Importance of the eastern Alaskan Beaufort Sea to feeding bowhead whales 1985–86, p. 449–479. Rep. to U.S. Minerals Manage. Serv. by LGL Ecol. Res. Assoc. Inc., NTIS No. PB88-150271.

[39] Berzin, A. A., V. L. Vladimirov, and N. V. Doroshenko. 1985. The distribution and numbers of cetacea in the Okhotsk Sea: results from aerial surveys. Int. Whal. Comm. Unpubl. Doc. SC/37/O5, 7 p.

[40] Tarpley, R. J., G. G. Stott, R. F. Sis, M. J. Shively, and G. H. Jarrell. 1985. Further observations on the morphology of the reproductive tract of the bowhead whale, *Balaena mysticetus*. *In* T. F. Albert (Editor), Third conference on the biology of the bowhead whale, *Balaena mysticetus*: extended abstracts and panel discussion, Anchorage, p. 115–119.

[41] Tarpley, R., R. Weeks, and G. Stott. 1988. Observations on reproductive morphology in the female bowhead whale (*Balaena mysticetus*). Int. Whal. Comm. Unpubl. Doc. SC/40/PS8, 50 p.

[42] Best, P. B., and H. Rüther. 1989. Aerial photogrammetry of southern right whales—a preliminary report. Int. Whal. Comm. Unpubl. Doc. SC/41/PS4, 18 p.

[43] Nerini, M. K. 1983. Age determination techniques applied to mysticete whales. M.S. thesis. Univ. Wash., 51 p.

harvested whales, suggest that bowhead whales may live >50 years (Philo et al., 1993) or >75 years (George et al., 1995).

Results from female bowhead whales examined for corpora albicantia or corpora lutea indicate sexual maturity begins when whale lengths exceed 14.2 m, and perhaps as small as 12.3 m (Nerini et al., 1984; Tarpley et al.[41]). Aerial photogrammetry indicates whales as small as 12.2 m were accompanied by calves (Davis et al.[22]). Smaller females tend to calve later in the spring migration than larger females: 1.5% (1/68) of the adults with calves photographed in the spring were <13.5 m long compared to 12% (7/59) in the summer (Koski et al., 1993). There is virtually no information on size at maturation for males, except that, in general they tend to be smaller than females (Nerini et al., 1984).

Using aerial photogrammetric techniques, Angliss et al. (1995) summarized and revised results from surveys conducted from 1985–92 (originally reported in Nerini et al.[31]; Withrow and Angliss, 1992; 1994). These show that 5.2% of the sampled population of bowhead whales in the Barrow area in the spring were calves (<6 m), 53.7% were juveniles (6–13 m), and 41.1% were adults (>13 m). These authors also showed that age segregation occurred during the spring migration: 80% of the measured animals early in the migration were juveniles, dropping to 20% by the end of the migration. Adults with calves did not appear until the last few weeks of the migration. This seasonal pattern was also evident in aerial photographic data showing increased degrees of graying on the peduncles (a sign of aging) as the migration season progressed (Rugh, 1990) and in sizes of whales harvested at Barrow (George et al., 1995). Cubbage and Calambokidis (1987) described segregation of bowheads by size in the Beaufort Sea, further confounding efforts to representatively sample the population for calving rates. On the other hand, Clarke et al. (1987) found little analytical evidence of geographic or temporal segregation of calves during the fall migration.

Population modeling by Breiwick et al. (1984) underlined the need for improved estimates of calf production and proportion of immature whales in the population. For modeling purposes, Chapman (1984) used an estimated crude birth rate of 0.072 (S.E. 0.014). Koski et al. (1993) reviewed available aerial photogrammetric data along with rates of sightings of calves from ice-based observers. These data suggested variable recruitment in bowheads with a 3–4 year cyclicity (also described in Rugh et al., 1992; Withrow and Angliss, 1992). The mean crude birth rate for all available information from 1982–89 (summarized in Koski et al., 1993:264) was 0.052. Even with this low birth rate, the Bering Sea bowhead population is increasing, suggesting a low rate of mortality (Koski et al., 1993; Whitcher et al.[44]).

Morbidity and Mortality

Although bowhead whale mortality caused by the subsistence harvest is fairly well documented (see section on Distribution and Abundance), particularly since 1977 in the Bering Sea stock, little is known about naturally occurring diseases and death in bowhead whales (e.g., Heidel and Albert, 1994). Since 1964, at least 36 cases exist in which the cause of death could not be established (Philo et al., 1993). Some of these deaths may be the result of hunter-inflicted wounds. Types of human-induced injuries include embedded shrapnel and harpoon heads from hunting attempts, rope and net entanglements from harpoon lines and crab pots, and collisions with vessels, summarized in Philo et al. (1993). Bowhead whales frequently react to being struck with a harpoon by rotating rapidly (Philo et al., 1993). This type of reaction near ropes or nets would only increase the likelihood of entanglement. Whales with ropes caught in their baleen and with scarring caused by rope entanglement have been observed during the harvest (Philo et al., 1992) and in aerial photographs of live animals (NMML, unpubl. data). Although incidental take of bowhead whales is apparently rare, there has been one reported entrapment and death of a young bowhead whale in a fishing net in Japan (Nishiwaki and Kasuya, 1970) and another in the waters of northwest Greenland in a net used to capture beluga whales (Kapel, 1985). Between 1976 and 1992, only three ship-strike injuries were documented out of a total of 236 bowhead whales examined from the Alaskan subsistence harvest (George et al., 1994). These low numbers suggest that either bowhead whales do not often encounter vessels, avoid interactions with vessels, or that interactions usually result in the death of the animal. Exposure to man-made noise and contaminants may produce short- and long-term effects (Richardson and Malme, 1993; Bratton et al., 1993) that may compromise the health and reproductive performance of some whales. The effects of repeated encounters with seismic vessels, drill rigs, hydrocarbons, and heavy metals are unknown. Anthropogenic impact is a function of the extent that industrial activities coincide with the bowhead whales' seasonal occupation of certain regions and the whales' tolerance level of the impacts (Richardson and Malme, 1993; Bratton et al., 1993).

It is not known whether bowhead whales suffer from stress-induced bacterial infections similar to those observed in captive cetaceans (Buck et al., 1987). Studies of harvested bowhead whales have provided information on bacterial, mycotic, and viral infections but not the level to which they contribute to mortality and morbidity (Philo et al., 1993). Skin lesions, found on all harvested bowhead whales, were not malignant or contagious. However, potentially pathogenic microorganisms inhabit these lesions and may contribute to epidermal necrosis and the spread of disease (Shotts et al., 1990). Exposure of these roughened areas of skin to environmental contaminants, such as petroleum products, could have significant effects (Shotts et al., 1990; Albert[45]); although, Bratton et al. (1993) con-

[44] Whitcher, B., J. E. Zeh, D. J. Rugh, W. R. Koski, and G. W. Miller. 1996. Estimation of adult bowhead whale survival rates. Int. Whal. Comm. Unpubl. Doc. SC/48/AS12, 22 p.

[45] Albert, T. F. 1981. Some thoughts regarding the possible effect of oil contamination on the bowhead whale, *Balaena mysticetus*. *In* T. F. Albert (Editor), Tissue structural studies and other investigations on the biology of endangered whales in the Beaufort Sea, p. 945–953. Rep. to Bur. Land Manage. from Dep. Vet. Sci., Univ. Md., Coll. Park, NTIS Accession No. PB86-153566.

cluded that such encounters were not likely to be hazardous.

Of 130 bowhead whales examined between 1980 and 1989, only one whale had a tumor, though this may be the result of incomplete necropsies performed on the other whales (Migaki and Albert, 1982; Philo et al., 1993). The tumor, located on the liver, was benign. According to Philo et al. (1993:295), "it is unlikely that tumors are major contributors to bowhead whale morbidity or mortality." Marine caliciviruses first discovered in California sea lions, *Zalophus californianus californianus*, are known to be widespread and transferable between terrestrial and marine hosts (Smith et al., 1986; Barlough et al., 1986; Smith et al., 1987; Smith et al.[46]). Though not isolated from bowhead whale tissues, there is evidence that these whales may be hosts for these viruses (Smith et al., 1986; Smith et al., 1987; Smith et al.[47]). Symptoms of calicivirus infection include formation of cysts, open sores, inflammation of the lungs, brain, heart, and stomach and intestine lining, and abortion (Barlough et al., 1986; Smith et al., 1986; Smith et al., 1987; Smith et al.[46]). How much these viruses contribute to natural mortality and possibly to reduced reproduction in the bowhead whale population is unknown (Philo et al., 1993).

Evidence of ice entrapment and predation by killer whales, *Orcinus orca*, has been documented in almost every bowhead whale stock. The percentage of whales entrapped in ice is considered to be small, given that this species is so strongly ice-associated (Tomilin, 1957; Mitchell and Reeves, 1982; Nerini et al., 1984; Philo et al., 1993). The ice may also provide some protection from killer whale attacks. The frequency of attacks is unknown and killer whale distribution in northern waters has not been well documented (George et al., 1994). In the Davis Strait stock, about one-third (5 of 16) of the summer residents photographed in Isabella Bay showed evidence of killer whale scarring along their flukes and sometimes their flippers (Finley, 1990). Two attacks were witnessed during Finley's study and appear to occur frequently; Inuit hunters even have a phrase for the behaviors observed during an attack, "Ardlingayuq." Of 195 whales examined during the Alaskan subsistence harvest (1976–92), 8 had been wounded by killer whales (George et al., 1994). Seven of the eight bowhead whales were greater than 13 m in length, suggesting either that scars are accumulated over time, or young animals do not survive a killer whale attack. Hunters on St. Lawrence Island reported two small (<9 m) bowhead whales found dead as a result of killer whale attacks (George et al., 1994). Overall, the frequency of attacks on bowhead whales in the Bering Sea stock appears to be low (George et al., 1994). Attacks witnessed in the Okhotsk Sea at the turn of the century are reported in Mitchell and Reeves (1982). Recent accounts include information on the distribution and abundance of killer whales in the Okhotsk Sea, but additional attacks have not been reported (Vladimirov, 1994). From the available data, it is not possible to assess the level of depredation on bowhead whales by killer whales, particularly in terms of size-class selection and encounter rates.

Management

Clearly, bowhead whale stocks are slow to recover, and some might not recover at all. The Spitsbergen stock was reduced from 24,000 to a few "tens" of whales and has not recovered in the past 80 years. The Davis Strait and Hudson Bay stocks declined from about 12,300 whales to less than 450 currently, although significant whaling has not occurred in 80 years. The Okhotsk Sea stock was originally around 3,000 whales, but after severe whaling which ended over 100 years ago, there are still only 300–400 whales. The Bering Sea may have had a stock that was eliminated, except for the component that migrated to the Beaufort Sea. This stock was reduced from at least 10,300 animals, and has been recovering slowly over the past 80 years to a current population of about 8,000. There is evidence that bowhead whales are long-lived animals. It is therefore possible that in the greatly reduced stocks, some of the animals have survived nearly since the termination of commercial whaling, but fecundity rates are so low that very few new whales are being added to the respective stocks. Calving intervals of 3–4 years and the possibility that bowheads whales do not become sexually mature until they are 20 years old may, in part, explain these slow recovery rates in stocks with only a few hundred whales.

The IWC is the primary body responsible for conservation and management of bowhead whale populations worldwide. All stocks of bowhead whales are classified as "protected" by the IWC. As mentioned in the Introduction, the United States further classified all bowhead whales as endangered under the ESA and depleted under the MMPA. Currently, the bowhead whales in the Bering-Chukchi-Beaufort Seas represent the largest surviving stock. This is the only stock, mandated by the IWC and through exemptions under the ESA and MMPA, still harvested by aboriginal hunters in Alaska. Thus far, a quota to harvest bowhead whales from the Bering Sea stock and the other stocks has not been provided to Russian or Canadian natives by the IWC (Stoker and Krupnik, 1993; IWC, 1995). As determined by the IWC's Scientific Committee, "the total of whales landed in the four years 1995–98 should not exceed 204, with a maximum number of 68 strikes in 1995, 67 in 1996, 66 in 1997, and 65 in 1998." (IWC, 1995:22). Any unused portion of the strike quota will be carried forward from that year and added to the strike quota of any subsequent years, provided that no more than 10 strikes are added to the strike quota for any one year. The average number of whales harvested per year

[46] Smith, A. W., D. E. Skilling, and K. Benirschke. 1981. Investigations of the serum antibodies and viruses of the bowhead whale, *Balaena mysticetus*. *In* T. F. Albert (Editor), Tissue structural studies and other investigations on the biology of endangered whales in the Beaufort Sea, p. 233–254. Rep. to Bur. Land Manage. from Dep. Vet. Sci., Univ. Md., College Park, NTIS No. PB86–153566.

[47] Smith, A. W. 1979. Serum antibodies and viruses. *In* J. J. Kelley and G. A. Laursen (Editors), Investigation of the occurrence and behavioral patterns of whales in the vicinity of the Beaufort Sea Lease Area, p. 445–457. Rep. to Bur. Land Manage. from Nav. Arctic Res. Lab., Barrow, Alaska, NTIS No. PB86-153582.

from 1989 to 1993, including those struck and lost, was 42 (Suydam et al., 1995).

Since 1981, the harvest has been monitored by the Alaska Eskimo Whaling Commission (AEWC) through a Cooperative Agreement with the National Oceanic and Atmospheric Administration (NOAA). This Cooperative Agreement will remain in effect until the year 2000. Also since 1981, the AEWC has channeled funds to the North Slope Borough (NSB) for censusing the bowhead whale population as it migrates past Point Barrow in the spring (Montague, 1993). The AEWC has also been responsible for allocating IWC quotas among its member communities and has worked to improve hunting methods and technology to reduce the number of whales struck but lost. Emphasis has been placed on promoting understanding of the needs of native Alaskan whalers and obtaining quotas that will meet these needs while still ensuring recovery of the bowhead whale population. Roles have included habitat management and protection in light of increased commercial activity in the Arctic (Stoker and Krupnik, 1993).

Under the 1994 reauthorization of the MMPA, the National Marine Fisheries Service (NMFS) and U.S. Fish and Wildlife Service (USFWS) developed a method for establishing minimum allowable incidental takes of marine mammals by commercial fisheries. This potential biological removal level (PBR) is defined as "the maximum number of animals, not including natural mortalities, that may be removed from a marine mammal stock while allowing that stock to reach or maintain its optimum sustainable population" (Marine Mammal Commission[48]). Using the minimum population estimate (N_{min}) of 7,524 bowhead whales for the Bering Sea stock, one-half the maximum theoretical net productivity rate ($0.5R_{max}$) of 4%, and a recovery factor (F_r) of 0.5, resulted in a PBR of 75 animals from the current population (Small and DeMaster[49]). Because the Alaska Eskimo subsistence harvest "is managed under an international regime that differs from the MMPA amended legislation," the IWC quota supercedes any quotas set by the MMPA(Small and DeMaster[49]). Reviews of observer data and vessel logbooks indicate that no incidental takes of bowhead whales by commercial fisheries have occurred in U.S. waters (Small and DeMaster[49]). Incidental takes of bowhead whales in fisheries have rarely been reported and are thought to not be an issue of concern; in particular because the habitat selected by bowheads (ice-covered seas) limits commercial or sport fisheries activities (Small and DeMaster[49]).

Impacts from industrial development (particularly offshore oil extraction) are of concern as most habitat of the Bering stock of bowheads is within active or potential lease zones. But studies indicate that bowhead behavior is often temporarily affected when exposed to close approaches by ships, seismic vessels, and aircraft. Reactions are less obvious when the noise source is fairly constant, such as with distant seismic or drilling work, but migrating bowheads sometimes adjust their course to divert around stationary sources of man-made noise (LGL and Greeneridge[50], Hall et al.[51], Richardson et al.[52]). Although there has been concern expressed by residents of the Arctic (Ahmaogak, 1985; Ahmaogak[53]), there is insufficient evidence about cumulative and long-term effects of anthropogenic noises (Richardson and Malme, 1993). The spring season appears to be a particularly critical period in the bowheads' annual cycles as this is the time all, or most, of the population migrates, often into areas covered by dense ice, where migration routes are constrained and most likely to be blocked by noise sources (Richardson et al.[52]). Conception and parturition happen during the spring, as well as some feeding. This is also the season of the most intense harvest by subsistence hunters.

Currently, bowhead whales in the Bering Sea are classified as a "strategic stock" under the amended MMPA. Stocks are classified as strategic when one of the following three criteria are met: 1) "level of direct human-caused mortality exceeds the potential biological removal level"; 2) "based on the best available scientific information, [the stock] is declining and is likely to be listed as a threatened species under the Endangered Species Act of 1973 within the foreseeable future"; or 3) [the stock] "is listed as a threatened or endangered species under the Endangered Species Act of 1973 (16 U.S.C. 1531 et seq.), or is designated as depleted under this act" (Marine Mammal Commission[48]). The level of human-caused mortality and serious injury during the subsistence harvest of Bering Sea bowhead whales, 42 animals per year, does not exceed the PBR nor the IWC quota for 1995. The lower end of the optimum sustainable population (OSP) range was calculated to vary between 6,500 and 10,500, using an initial stock size of 12,599 (95% C.I. 10,945–17,431)(IWC, 1995) and the assumption that the maximum net productivity level (MNPL) is 60% of carrying capacity (K). Objective criteria for defining when this population should be downlisted to threatened or delisted under the ESA have not been developed to date.

48 Marine Mammal Commission. 1995. The Marine Mammal Protection Act of 1972, as amended. Mar. Mamm. Comm., 1825 Conn. Ave. N.W., Wash. D.C. 20009, 299 p.

49 Small, R. J., and D. P. DeMaster. 1995. Alaska marine mammal stock assessments 1995. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-AFSC-57, 93 p.

50 LGL and Greeneridge. 1987. Responses of bowhead whales to an offshore drilling operation in the Alaskan Beaufort Sea, autumn 1986. Rep. for Shell W. E. P. Inc., Anchorage, Alaska, from LGL, Ltd., King City, Ont., Can., and Greeneridge Sci. Inc., Santa Barbara, Calif, 371 p.

51 Hall, J. D., M. L. Gallagher, K. D. Brewer, P. R. Regos, and P. E. Isert. 1994. ARCO Alaska Inc. 1993 Kuvlum exploration area site specific monitoring program: final report. Rep. for ARCO Alaska Inc., Anchorage, from Coastal Offshore Pac. Corp., Walnut Creek, Calif., 219 p.

52 Richardson, W. J., C. R. Greene Jr., J. S. Hanna, W. R. Koski, G. W. Miller, N. J. Paternaude, and M. A. Smultea. 1995. Acoustic affects of oil production activities on bowhead and white whales visible during the spring migration near Pr. Barrow, Alaska—1991 and 1994 phases. Rep. for U.S. Minerals Manage. Serv. from LGL, Ltd., King City, Ont., Can. OCS Study MMS 95–0051, 539 p.

53 Ahmaogak, G. 1989. Protecting the habitat of the bowhead whale. *In* L. Rey and V. Alexander (Editors), Proceedings of the sixth conference of the Comite Arctique International, New York, 13–15 May 1985, p. 593–597.

The agency plans to develop objective criteria to determine whether this stock's current classification is accurate or, if not, whether it should be listed as threatened or removed from the list of endangered and threatened wildlife. One possible approach which will be investigated is that used by IUCN-World Conservation Union. This system of classification consists of three levels (i.e., critical, endangered, and vulnerable), each level representing a different probability of extinction within a specific period of time (Mace and Lande, 1991). The IUCN criteria also take into account extent of occurrence, area of occupancy, number of locations or subpopulations, and number of mature animals. Additional objective criteria based on recently revised Recovery Plans, as appropriate, will also be considered. Because population estimates are extremely low for the Spitsbergen, Davis Strait, Hudson Bay, and Okhotsk Sea stocks, these should continue to retain endangered status.

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Temporal Changes in a Tropical Nekton Assemblage and Performance of a Prawn Selective Gear

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Introduction

Certain aspects of the ecology of many trawlable nekton assemblages or communities in the warmer Indo-West Pacific subregions have been published in detail. Geographically, most of these associations are in habitats situated in the vicinity of either the often heavily urbanized or fished centers (Chua, 1973; Richards and Wu, 1985; Quinn and Kojis, 1986; Pinto, 1988; Weng, 1988; Shaw et al., 1990) or the ecologically alterable areas in connection with industrial or fishery development (Blaber, 1980; Quinn, 1980; Rainer and Munro, 1982; Rainer, 1984; Salini et al., 1994). The results of some of these and allied studies are often used to test the hypotheses of latitude gradients in species diversity and stability-time-disturbance features of benthic marine communities (Pianka, 1966; Sanders, 1969; Slobodkin and Sanders, 1969; Dayton and Hessler, 1972), with various degrees of success as illustrated by Richards and Wu (1985) and Quinn and Kojis (1986).

Situated well in the center of the Indo-Pacific, Papua New Guinea (PNG) has a very poor freshwater fish fauna (Munro, 1972; Berra et al., 1975; Roberts, 1978; Allen and Coates, 1990), but is extremely rich in the marine counterpart. Kailola (1987) recently revised the number of New Guinean (fish) species to nearly twice the 1,096 species recorded in the monumental work of Munro (1967). Meanwhile, except for a relatively few localities under current large-scale mining effects (Pernetta, 1988; Hughes, 1989), the aquatic environment in PNG is pristine (Apte et al., 1991). These biological features have motivated this study. On the component characteristics and perhaps species diversity, our attention is focused on the assemblage-oriented approach on fishes of Tyler (1971).

The primary goal of this study was to demonstrate our concern with trawl bycatch in general (Saila, 1983; Alverson et al., 1994) and prawn bycatch in particular (FAO-IDRC, 1982). Up to 50,000 t of finfish are trawled and then dumped as bycatch by prawn trawlers in the Gulf of Papua and Torres Strait annually (Watson, 1984; Pender and Willing, 1989; Harris and Poiner, 1990). These practices can affect wise resource use, sound prawning economics, or both (FAO-IDRC, 1982; Somers, 1990). Unfortunately the bioeconomic benefits of a variety of prawn selective gears tested for bycatch reduction elsewhere over 25+ years (Seidel, 1975) have been ignored by many, except Indonesian (Sujastani, 1984), fisheries-concerned personnel in the Indo-West Pacific. For example, in a 1990 special issue on "the effect of fishing," mainly prawning (Aust. J. Mar. Freshwater Res. 41 (1): 1–197), no mention is made of the positive effect of several important types of selective gears intensively developed in the North Sea and, especially, the Gulf of Mexico from the early 1970's. De-

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ABSTRACT—The temporal variation of components of a moderately diverse (H=*1.46) tropical estuarine fish assemblage (long. 146°30'E, lat. 8°45'S) was directed by salinities that had been determined by local oceanographic and probably topographic conditions. For this assemblage, two types of intrayear component profiles are predicted. Pooled data (1988–91) reveal a large component of regular/resident species (43%) in an assemblage which has been under a narrow temperature regime (<5°C). These results facilitate a discussion on the relevance and usefulness of three hypotheses often cited in studies concerning species diversity and component characteristics of the subtropical/tropical coastal nonreef fish assemblages.*

Manifestations of the assemblage are reflected in catch composition and weights of 39 trials conducted for a selective prawning gear whose performance in bycatch reduction, mainly for finfishes, is judged by an index, E, *we have previously proposed. This gear is capable of harvesting the prawn while conserving the demersal fish. Behavioral responses to netting of the prawns and the finfishes, especially the nearshore surface schoolers such as leiognathids, are discussed from several points of view. An adaptation in terms of group selection for leiognathids of their locking mechanism of median fin spines has been interpreted. For the purpose of bycatch reduction or* E *enhancement, suggestions for improvements in net design and trawl configuration by considering the behavioral features of fish are made. Our original formula of* E *is modified for general use.*

Bycatch problems in the regional prawn fisheries and their possible impacts on fishery planning and development in Papua New Guinea as a developing country are discussed. The gear tested may offer enormous ecological and economic benefits. The gear is multipurpose, extremely simple, and can also be used as a biological sampler.

velopment in the latter region from the mid-1970's, led by J. W. Watson, Jr. (1989), was instrumental, we believe, in the eventual ruling of the U.S. Government in June 1987 to require prawn trawlers to use conservation measures, e.g. selective gears, while trawling in southern and southeastern U.S. waters.

This paper first deals with the bycatch, composed primarily of finfish, in nets trawled by a prawn-selective gear under paired conditions in 39 trials made near Yule Island in the Gulf of Papua in November 1988 and April 1989–91. Information derived from the bycatch is used to analyze a nekton assemblage and performance of the gear tested. Finally, attempts are made to apply the results to several aspects on temporal changes in the tropical and subtropical demersal fish assemblages and on reduction and utilization of bycatch in the regional prawn fisheries.

Materials and Methods

Yule Island (long. 146°30'E, lat. 8°45'S) is about 150 km northwest of Port Moresby and 300 km southeast of major commercial prawn grounds (Fig. 1). Sea work was conducted once a year from 1988 to 1991 aboard the *Scomber* (5 GT, 12 m long), concurrent with an annual week-long practical cruise for students in fisheries (Kan et al., 1989; Matsuoka et al., 1991).

The study area is about 5 km northwest of Yule Island and open seaward to the west. Two tributaries of the Angabunga River system enter from north with their plumes visible up to 5 km from shore. The total study area in this open estuary is about 10 km^2. The general area is known as a traditional prawn ground but has been off limits to all vessels in the commercial prawn fleet. Ecologically, it is mostly undisturbed.

The structure of the trial net was described in detail by Kan et al. (1989) and Matsuoka and Kan (1991). The net was designed to hold a device which was expected to perform a similar function to the "Trawling Efficiency Device" or TED in several prawn gears tested intensively in the Gulf of Mexico (Watson et al., 1986; Watson and Taylor, 1986; Watson, 1989).

Our TED (Kan et al., 1989; Matsuoka and Kan, 1991) had two side windows which were closed with small net pieces in about half of the trawls conducted. When closed, the net would behave the same as a typical bottom trawl net. Therefore, there were a pair of trawling conditions: "TED-open" and "TED-closed." This enabled us to compare catches hauled under opposite circumstances, i.e. with and without the TED, using one gear. The TED was 165 × 85 × 85 cm in length, breadth, and height, respectively.

The net was dragged for 30 minutes at 1.5–2 knots (2.8–3.9 km/hour) during daytime. Hauled fishes and prawns were sorted immediately into taxonomic groups, often to the family level, and then weighed. Sample specimens were preserved in ice for later laboratory studies. Except for the prawns and larger edible finfishes, all other fishes hauled were eventually discarded. However, two 1991 TED-closed hauls were fully retained for a complete analysis of bycatch species composition.

Oceanographic data were taken before, during, and after a trawl on most occasions. The instruments used for in situ measurements were a 1 liter Van Dorn Sampler[1] (Yugosha) for water samples, a refractometer (ATAGO S/Mill 0–100‰) and Cole-Parmer Water Instrument (#5946) for salinities, a bottom sampler (Yugosha) for sediments, a current meter (Toho-Denton CM-1A) for currents 1 m below surface, and a vessel-fixed echo sounder (Furuno FE600) for depth. The direction of currents was determined by reading the degree of compass bearing.

Identification of the prawns and fishes was aided by Grey et al. (1983), Munro (1967), Masuda et al. (1984), and Kailola (1987). The species diversity index, H (Shannon and Weaver, 1963), was calculated from

$$H = -\sum\left(\frac{n_i}{N}\right)\ln\left(\frac{n_i}{N}\right) \qquad (1)$$

the dominance index, c (Simpson, 1949; Peet, 1974), from

$$c = \sum\left(\frac{n_i}{N}\right)^2 \qquad (2)$$

and the evenness index, e (Pielou, 1966), from

$$e = \frac{H}{\ln S} \qquad (3)$$

where n_i is the number of individuals of the ith species, N is the number of total individuals of all species, and S, is the total number of species observed.

In the analysis of catch composition, all statistical tests were applied at the 95% significance level unless stated otherwise. An index of gear performance in bycatch reduction, E (Kan et al., 1989; Matsuoka and Kan, 1991), was calculated from

$$E(\%) = \frac{F_c - F_o}{F_c} \times \frac{P_o}{P_c} \times 100 \qquad (4)$$

where F stands for the catch weight of finfishes, P for that of prawns, c for a TED-closed condition, and o for a TED-open condition.

Results

Oceanographic Parameters

Trawls were made to transect a portion of a plume about 1.5 km from shore. The sea surface in the trawling area was green to light green and brown. Water temperatures ranged from 27°C to 30°C and salinities from 7‰ to 28‰ (mean 12.1‰) during 1988–90 (Table 1). The area was shallow, 8–12 m, with a soft deposit type of bottom.

Bottom salinities, measured in 1991 only, were high, ranging from 34.8‰ to 35.7‰. Surface salinities of the year were relatively high (mean 25.2‰). Mean current speed was 0.25 m/sec (5.12 n.mi./day). The current directions were mainly southeastward (295°–325°) (Table 1).

Trawled Animals in General

The trawled animals consisted of a target catch of four penaeids (*Penaeus merguiensis*, *P. monodon*, *Metapenaeus endeavouri*, and *M. ensis*) and a bycatch

[1] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

Table 1.—Oceanographic parameters recorded near Yule Island in northeastern Gulf of Papua. Note: Data were collected in mid-November 1988, early to mid-April 1989–90, and on 9 April 1991.

Item	No. of records	Range 1988–89	1990	1991	Mean
Temperature (°C)					
Air	39	26–35	26–35		30.84
Surface	43	27–30	27–30	29–30	28.85
Bottom	4			29 (all)	29.00
Salinity (‰)					
Surface	43	7–28	7–21	22–27	18.71
Bottom	4			35–36	35.40
Current	4				
Speed (m/sec)				0.15–0.35	0.25
Direction (compass degrees)	4			295–325	310

Table 2.—Finfishes caught by TED-open and TED-closed trawls northwest of Yule Island in the northeastern Gulf of Papua.

Family and species caught, 1988–91	TED-closed catch (1991) Notation[1]	No. of fish	Percent of fish
Carcharhinidae			
Carcharhinus macloti	R	1	0.02
Sphyrnidae			
Sphyrna lewini	P		
Dasyatidae			
Dasyatis bennetti	P, NR		
Himantura uarnak	P		
Gymnuidae			
Aetoplatea tentaculata	P		
Clupeidae			
Anodontostoma chacunda	P		
Herklotsichthys sp.	P		
Sardinella albella	R, ON	1	0.02
Sardinella melanura	O	3	0.05
Engraulidae			
Setipinna tenuifilis	P		
Thryssa aestuaria	R	3	0.05
Thryssa hamiltonii	R	4	0.07
Thryssa sp.	R	1	0.02
Synodontidae			
Saurida tumbil	O, ON	1	0.02
Synodus variegatus	P		
Ariidae			
Arius armiger	R	151	2.52
Plotostidae			
Plotosus canius	P		
Antennaridae			
Kuiterichthys furcipilis	P, NR		
Fistularidae			
Fistularia petimba	P		
Platycephalidae			
Platycephalus indicus	P		
Pegasidae			
Pegasus volitans	O, ON	3	0.05
Teraponidae			
Terapon jarbua	R	12	0.20
Terapon theraps	R	44	0.73
Priacanthidae			
Priacanthus macracanthus	R	3	0.05
Apogonidae			
Archamia lineolata	P		
Sillaginidae			
Sillago sihama	R	3	0.05
Lactariidae			
Lactarius lactarius	R	19	0.32
Carangidae			
Alectis indicus	P		
Carangoides chrysophrys	O, ON	2	0.03
Caranx para	R	1	0.02
Caranx sexfasciatus	R	8	0.13
Megalaspis cordyla	R	1	0.02
Parastromateus niger	P		
Scomberoides commersonianus	R	2	0.03
Scomberoides lysan	P		
Scomberoides tol	P		
Selar boops	O, ON	3	0.05
Selaroides leptalepis	O, ON	3	0.05
Ulua mentalis	P		
Menidae			
Mena maculata	P		
Leiognathidae			
Gazza minuta	R	304	5.07
Gazza sp.	P		
Leiognathus rapsoni	R	147	2.45
Leiognathus splendens	R	3,760	62.70
Secutor ruconius	R	622	10.37
Lutjanidae			
Lutjanus erythopterus	P		
Lutjanus johnii	P		
Lutjanus semicinctus	P		
Nemipteridae			
Nemipterus marginatus	P		
Nemipterus sp.	P		
Gerreidae			
Gerres filamentosus	P		
Pomadasyidae			
Pomadasys argenteus	P		
Pomadasys argyreus	R	584	9.74
Pomadasys maculatum	P		
Sciaenidae			
Johnius (Johnieops) goldmani	R	25	0.42
Johnius (Johnieops) amblycephala	P		
Johnius (Johnieops) belangerii	R	20	0.33
Johnius (Johnieops) macropterus	P		
Nibea soldado	P		
Otolithes ruber	R	84	1.40
Protonibea diacanthus	P		
Mullidae			
Upeneus sulphureus	R	94	1.65
Upeneus tragula	P		
Drepanidae			
Drepane longimana	P, NR		
Drepane punctata	R	43	0.72
Cirrhitidae			
Cirrhitichathys falco	P		
Sphyraenidae			
Sphyraenells flavicauda	P		
Polynemidae			
Polydacttylus microstoma	R	2	0.03
Polydactylus sealei	R	6	0.10
Trichiuridae			
Trichiurus lepturus	R	15	0.25
Sombridae			
Scomber japonicus	O, ON	4	0.07
Bothidae			
Pseudorhombus elevatus	R	3	0.05
Cynoglossidae			
Cynoglossus bilineata	R	3	0.05
Triacanthidae			
Triacanthus indicus	R	4	0.07
Tetradontidae			
Arothron nigropunctatus	R, ON	2	0.03
Arothron sp.	R	6	0.10
Sphoeroides spadiceus	R		
Total 37 families and 77 species/forms		5,997	ca. 100

[1] Note: "NR" indicates a species new to Papua New Guinea, "ON" denotes a species only occurred in 1991, "O" is an occasional species, "P" is a periodic species, and "R" is a regular/resident species.

of many finfishes along with a few jellyfishes, gastropods, mantis shrimps, crabs, starfishes, and reptiles (one sea turtle and two sea snakes). Numerous silvery and mucous leiognathids were conspicuously on top of the bulk of hauled animals in each of the catches. Three dasyatid stingrays were trawled on different occasions during 1989–90; they were excluded from the comparison of finfish catches due to their anomalously large size (each >20 kg), which would bias the results. On many occasions, seabirds and sharks were observed scavenging the bycatch soon after it had been discarded.

Trawled Fishes

A total of 77 species in 37 families were identified (Table 2). Three were new records for PNG: stingray, *Dasyatis bennetti* (specimen disc width 650 mm); frogfish, *Kuiterichthys furcipilis* (specimen TL 53 mm); and batfish, *Drepane longimana* (specimen TL 168 mm). *Cirrhitichthys falco* appears to be new to the record of fishes from the Papuan Gulf. One form in each of the five genera, *Herklotsichthys*, *Thryssa*, *Gazza*, *Nemipterus*, and *Arothron*, was of uncertain taxon.

Among the 37 families, Carangidae had more than 10 species, Sciaenidae had seven species, Clupeidae, Engraulidae, and Leiognathidae each had four species, and Lutjanidae and Pomadasyidae each had two species. The remaining 30 families were all monospecific.

Eight species were found only in 1991: *Sardinella alebella*, *Saurida tumbil*, *Pegasus volitans*, *Carangoides chrysophrys*, *Selar boops*, *Selaroides leptalepis*, *Scomber japonicus*, and *Arothron nigropunctatus*.

From the 1991 TED-closed catch data, the abundance of individual species in each family was assessed (Table 2). Leiognathids were the most abundant group (about 80% of 5,997 fish trawled), followed distantly by pomadasyids (9.7%), ariids (2.5%), mullids (1.7%), and 18 other groups (about 6% combined). This profile yielded a diversity index (*H*) of 1.46, a dominance index (*c*) of 0.42, and an evenness index (*e*) of 0.28 for the assemblage in April 1991.

Finfish Catch vs. Trawling Condition

In addition to the four penaeids, most listed finfishes (Table 2) were found in

the majority of hauls in 1988–89. Minor fishes (Group 7 below) occurred less in 1990. In the 1991 TED-closed hauls, only one-half of the 77 species, in 22 of the 37 families, occurred (Table 2).

In terms of catch weight, the penaeid prawn and six finfish groups were distinguished in nearly all 1988–90 catches:

1) Penaeids (penaeid prawns),
2) Leiognathids (ponyfishes),
3) Pomadasyids (javelinfishes or grunts),
4) Polynemids (threadfins),
5) Sciaenids (jawfishes or drums),
6) Lactariid—*Lactarius lactarius* (milk trevally), and
7) All other finfish families.

This taxocene was tabulated for an analysis of catches from 13 pairs (TED-closed vs. TED-open) and 13 sets of weight data obtained, respectively, from the 1988–89 and 1990 trawls (Table 3).

As expected, the total and mean weights of the 13 TED-closed catches were considerably greater than those of the 13 TED-open ones (855 kg vs. 548 kg and 66 kg vs. 42 kg, respectively). However, the mean weight of prawns in these two types of trawls in 1988–89 (6.3 kg and 5.6 kg) was not significantly different (P<0.05). Also, the prawn retention ratio percentage, mean (open) / mean (closed) × 100, was extremely high, up to 98%, in 1990. Conversely, the mean exclusion ratio percentages (1 – retention ratio) × 100, of all finfish in a TED-open trawl were only 38% and 54%, respectively, in 1988–89 and 1990.

Fish catch weights under the two trawling conditions during 1988–90 were compared (Table 4). Leiognathids, caught repeatedly in very large quantities, showed no difference among all catches (P<0.05). Difference between the TED-closed and TED-open catches was significant for pomadasyids (P<0.05), but only slightly significant for either sciaenids or polynemids (P<0.1). However, it was noted that the sciaenids were completely absent from five, and, polynemids from two, of the 13 TED-open catches (Table 3). Other fishes (Group 7), in 32 families, contributed to this difference between two trawl types. *L. lactarius* occurred much more in the TED-closed catches of 1990 than those of 1988–89 (P<0.05).

Gear Performance

Pooled data for 1988–90 (Table 3) gave the present dual-condition gear a performance in bycatch reduction, E of 43%. The gear performed better in 1990 (51%) than 1988–89 (34%). This difference was caused by a large increase of the biomass of *L. lactarius* in catches in 1990 (Table 3). This fish fluctuated again in its abundance, in the opposite direction, the following year (Table 2).

Discussion

Temporal Variation of the Assemblage

We could only trawl a site within a particular week each year between 1988 and 1991. The area and time selected for the trawling therefore were extremely crucial (Johnson and Nielsen, 1985). The ecosystem northwest of Yule Island is known to be relatively undisturbed as well as unexploited. Our trawling was timed to a transition in direction of two trade winds prevailing the Gulf of Papua (Wyrtki, 1960): the "Lahara," northwest from December to March and the "Laurabada," southeast from late March–early April to late October. As the pattern of both surface and bottom currents there has been known to be generally parallel to that of the trade winds (MacFarlane, 1980), we expected to collect a good deal of data by sampling an assemblage which we believed was in a process of change in composition.

Without critically considering an effect of time lag, data collected at a particular period apply only to the fish assemblage congregated at the time of collection (Fay et al., 1978), here mainly one week in mid-April. For this study of fish and prawn selective trawl gear, data were collected through a program conducted intensively at a selected time and site (Kan et al., 1989; Matsuoka et al., 1991) and, hence, were judged important to show certain aspects of the fish/nekton assemblage then converged, as reflected by its characteristics shown in the TED-open and TED-closed catches.

Temporal change in trawl fish assemblages in various habitats has been studied since the late 1960's when the concept of fish assemblage was advancing (Tyler, 1971). Only abiotic factors (Marais, 1988) are considered, by concept. Salinity has been observed as a causative factor in maintaining intrayear (within year) and /or interyear (between years) variations in several estuarine and coastal fish/macrobenthos assemblages in PNG and Queensland, Australia (Stephenson, 1980; Quinn, 1980; Stephenson et al., 1982; Rainer, 1984; Quinn and Kojis, 1986; Weng, 1988). In April 1991, only half of the total number of fish species recorded during the study period (1988–91) occurred in the TED-closed catches (Table 2). This change is believed to be a consequence of the more saline water in 1991 than in each of the two previous years (Table 1).

Higher salinity than usual in the estuary could be caused by one or more of the following conditions: drought at higher altitudes, greatly reduced local rainfall, higher rate of local evaporation, inflow of oceanic water, or heavy influx of salt ions from anthropogenic sources. For this estuary in April 1991, the latter condition was impossible. The first two conditions could not be verified due to lack of local meteorological data; however, the general weather pattern along the Papuan coast indicated an absence of both conditions during March–April 1991. Daily air temperature varied very little in our records during 1988–90. However, based on our in situ observations of the current direction, a delay of the "Laurabada" was occurring in mid-April 1991 and, consequently, the "Lahara" together with the currents it drove continued to persist southeastward. As a result, there was an influx of oceanic waters, driven by the southeastward winds, into this open estuary. Our salinity records of two earlier years in April indicate that no such delay has taken place for either year (Table 1). Nevertheless, Yule Island itself should topographically subdue any major northwestward currents from reaching the estuary (Fig. 1).

Structure and function in a system of fish assemblages or communities are dynamic. Information on temporal

variation of the components are essential for ecological studies on such a system (Ross, 1986). Meanwhile, as pointed out by Tyler et al. (1982) and Caddy and Sharp (1986), present knowledge of the structure and function of fish/nekton associations should be consolidated and mapped for convenience in marine resource management (Munro, 1983; Butler et al., 1986).

Among the eight species that occurred only in 1991, seven are truly marine fishes: three carangids (Gunn, 1990) and one each, clupeid, scombrid, synodontid, and pegasid (Pietsch, 1978). They are designated as the occasional species of this assemblage; their occurrence has been coincident with an incursion of oceanic waters (34–35 ‰, "Type 3," Wolanski et al., 1984).

Our data are insufficient to shed further light on the remarkable interyear component change of this shallow water assemblage, as observed between 1988–89 and 1991. In our attempt to delineate the temporal component profile of the assemblage, two distributional records have been essential: a list of primarily estuarine fishes from two river deltas about 400 km northwest of Yule Island (Liem and Haines, 1977) and a record of trawlable teleosts from the Papuan Gulf in mainly offshore waters about 50 m deep (Kailola and Wilson, 1978). The data on the euryhaline elasmobranchs of Taniuchi et al. (1991) and the euryhaline teleosts of Roberts (1978), Collette (1983), and Quinn and Kojis (1986) from PNG are also helpful. By comparison, the status of temporal characteristics of nearly all present species in the assemblage can be inferred (Table 2).

Not surprisingly, none of the seven occasional species (9% of total number of species) is found in the above list of delta fishes, but all are in the record of Gulf fishes. About 33 (43%) species have occurred in catches throughout this study and hence designated as the resident or regular species of the assemblage. These are euryhaline species. Except *A. nigropunctatus*, caught only in 1991, all resident teleost species are found in the record of Gulf fishes. *Carcharhinus macloti* is the sole resident elasmobranch here. Its allied species, *C. carcharhinus* is highly riverine in PNG (Kan and Taniuchi, 1991). About 28 (85%) of the resident species or, in a few cases, their congenerics including the lutjanids, pomadasyids, and mullids, also occur in the Gulf deltas or similar habitats elsewhere in PNG. The remaining 37 (48% of the total number of species) species occurred intermittently during the study period and could be considered as the periodic species of this assemblage. These fishes should be more stenohaline and would move to less saline waters in the presence of oceanic water. About 22 (60%) of the periodic species are found in either the delta or the Gulf fish list mentioned above. There should be more periodic species in the delta list than in the Gulf record. However, the present figure (37) is acceptable because the latter list is considerably longer than the former (350+ species vs. 144 species), comprising only teleost species from a much greater zone covering many offshore and in particular nearshore/onshore subzones.

With valid data from four coastal or estuarine areas in the northwest Atlantic (lat. 38°N to lat. 45°N), Tyler (1971) hypothesized that a temperature range stabilizes the temporal components in fish assemblages. More regular or resident species would be expected to occur in an assemblage under a narrower temperature regime. Many studies of assemblages from several warmer temperate and subtropical coastal waters have supported this hypothesis to certain degrees, including Allen (1982) in southern California (lat. 34°N), Bennett (1989) in southwestern Cape, South Africa (lat. 34°S), Yoshiyama et al. (1982) in southern Texas (lat. 27°N), Quinn (1980) in southern Queensland (lat. 27°S), Jones and Chase (1975) in Guam (lat. 14°N), U.S.A., and Rainer and Munro (1982) in northwestern Queensland (lat. 17°S). Our assemblage (lat. 9°S), on an interyear basis during April 1989–91, was under a temperature regime less than 5°C wide, and had a very large component of resident species (43%). Quinn (1980) reported one tetradontid, *Spheroides pleurostictus*, as the only resident fish of an estuarine assemblage of 44 fishes (2.3%) with a 17°C wide annual temperature range. Richards and Wu (1985) listed 16 resident species in a bay assemblage immediately west of the island of Hong Kong (lat. 22°N) of 85 species (19%) with an annual temperature range of 12°C.

Bennett (1989) observed that the seasonal flooding and coastal topography impacted the annual component profile of three estuarine fish assemblages under a temperature range of 8°C. Quinn and Kojis (1986) related interyear component variation in an estuarine nekton assemblage in PNG where the temperatures ranged only 6°C due to local rainfall characteristics. Both rainfall and flooding affect local salinities (Stephenson, 1968; Lowe-McConnell, 1987). According to our study and Quinn and Kojis (1986), other weather-caused "anomalies" such as the intrusion of oceanic waters and local droughts may also affect salinities in the estuaries. Therefore, we suggest that in PNG the component characteristics of coastal nonreef fish assemblages are related to local salinities which in general are determined by a weather pattern that, in turn is controlled by the prevailing monsoons. Therefore, interyear variability, often unpredictable, may be superimposed upon predictable seasonality, in PNG and probably elsewhere in coastal areas of the tropics (Lowe-McConnell, 1987).

For the purpose of multispecies fisheries management, a holistic approach involving abiotic and biotic, including human, factors should be adopted in the study of temporal features of tropical demersal fish faunas for baseline information (Sainsbury, 1982; Gulland and Garcia, 1984; Longhurst and Pauly, 1987). Unfortunately, such studies from PNG are few. Dalzell (1987) reported a peaking in spawning intensity of two inlet engraulids associated with the monsoon seasonality in New Ireland. Recent relevant data on nearshore faunas in New Guinea include Erftemeijer and Allen (1990) and Nojima and Mukai (1990) on trophic relationships; Quinn and Kojis (1986) on indications of a mangrove-lined estuary as "safe site(s) (Frank and Leggett, 1983)"; Quinn and Kojis (1987) on some nek-

ton behavioral responses to abiotic parameters; and Sundberg and Richards (1984), Wright and Richards (1985), and Lock (1986) on fishing activities and effects.

Although the applicability of the Shannon-Weaver diversity index (H) to such habitats as the often heterogeneous coastal bottoms has been questioned (Pielou, 1966; Caddy and Sharp, 1986), the index is frequently used by fisheries ecologists (Routledge, 1979; Washington, 1984). As diversity of a community or assemblage depends upon not only the number of species but also the evenness of distribution of individuals among the species, H should be measured along with additional ecological measures including the dominance index (c) (Simpson, 1949; Peet, 1974) and the evenness index (e) (Pielou, 1966). Our assemblage, in mid-April 1991, exhibited an H value (1.46) smaller than that in three other tropical assemblages, in Guam, southern Taiwan, R.O.C., and the Philippines: 3.05, 3.15, and 1.98 respectively (Jones and Chase, 1975; Lee, 1980; Pinto, 1988), and even of assemblages in the subtropical Hong Kong and Queensland (1.90–2.25) (Quinn, 1980; Richards and Wu, 1985; Weng, 1988). Both the dominance (c) and evenness (e) indices, here, were moderate, respectively, 0.42 and 0.28, reflecting the role *Leiognathus splendens* played in the former (c) and leiognathids as a whole in the latter (e).

Our smaller value of H may be due partially to the large mesh size (4.5 cm) of the net used. Mesh sizes used in other demersal fish surveys of tropical/subtropical waters, excluding those for larval/juvenile fish (Allen et al., 1983), ranging from 2.5 cm (Gibbs and Matthews, 1981–2; Pinto, 1988) to 5.5 cm (Watson et al., 1990). However, the H value (1.46) we observed is for an assemblage in waters under a strong oceanic influence ("Type 3" waters/salinities; Wolanski et al., 1984). Weng (1988) reported a decrease of diversity (H) in trawlable fish assemblages on a gradient from an estuarine zone (2.0–2.5) to a central (bay) zone (1.4–2.0) and two oceanic zones (1.9–2.0 and 1.1–2.0) in the subtropical Moreton Bay, Queensland. Nevertheless, providing that the sampler (4.5 cm mesh), sampling (daytime only), and local topography remain similar to those herein, we predict a typical H value around 1.5 for any assemblages congregated between December and March ("Lahara" type) and a typical H value up to 3.0 for those between April and November ("Laurabada" type) in the estuary presently studied. Assemblages of the "Lahara" type would have a larger component of resident species congregated in the oce-

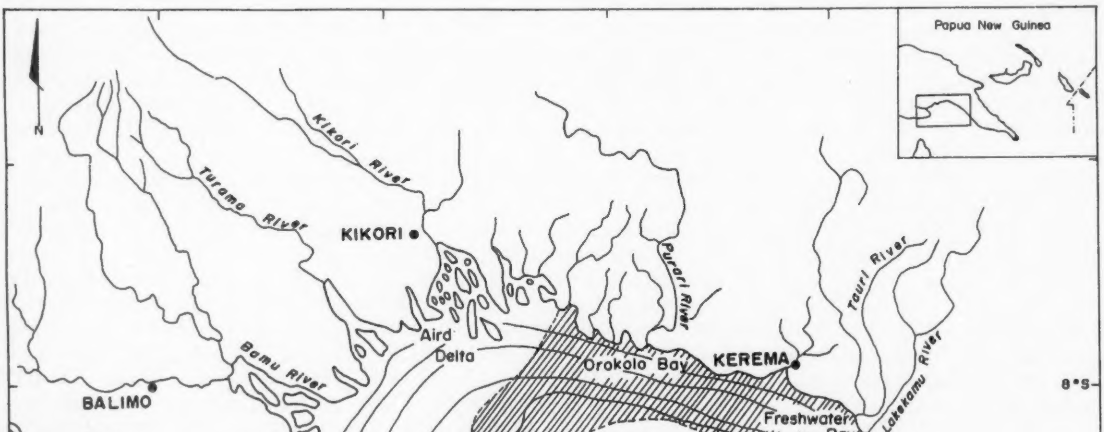

Figure 1A. — Commercial prawning grounds in the Gulf of Papua, PNG.

anic type waters while the "Laurabada" type would have a larger component of periodic species congregated in the estuarine-type waters.

In his interpretation and discussion of findings on the temporal profiles of several temperate and tropical demersal fish assemblages, Tyler (1971) made no reference at all to the then popular and seemingly relevant hypotheses of Pianka (1966) and Sanders (1969). Major works on the fish/macrobenthos associations in the southeast Asian and warmer Australian regions have similarly refrained (Chua, 1973; Blaber, 1980; Stephenson, 1980; Quinn, 1980; Rainer and Munro, 1982; Weng, 1988; Watson et al., 1990). This may be due to Pianka's (1966) use of the word "latitude," which is expressed for a totally artificial entity. It tends to be inconclusive and hence undesirable to test, with data derived from the spatially limited assemblages, those hypotheses that are of a general and mainly a faunal-region-scale manifestable nature.

For instance, in their attempts to present selected results either supporting or contradicting the hypothesis of Pianka (1966) and, perhaps, that of Sanders (1969) as well, Richards and Wu (1985) and Quinn and Kojis (1986) have conveniently used an entirely independent set of published data (see Fig. 8 in the former and Fig. 1 in the latter). The Tyler (1971) hypothesis on a manifestation of the effect of temperature regime is more prudent in elucidating the subject of component characteristics of fish assemblages.

As we have observed here, other causative factors such as salinity and topography should also be considered in drawing any conclusions on the component change and, perhaps, species diversity of coastal fish assemblages (Bennett, 1989), especially in the tropics. With reference to Quinn (1980), Quinn and Kojis (1986) discounted the effects of such factors existing in their study area for their comments apparently to contradict Pianka's (1966) concept. The two estuaries, Serpentine Creek in southern Queensland (lat. 17°S) and Labu lakes (lat. 7°S) in PNG, where Quinn sampled for those two publications, are different in salinity profile and especially topographic features. The latter, not described in Quinn and Kojis (1986), is unique in that those lakes are mostly separated from the sea by a narrow sandbar upon which several villages are situated, and the inflow of sea water to them is restricted to an opening less than 50 m in width (Apte et al., 1991). Fish assemblages in those two entirely and physically different habitats are hardly comparable in Pianka's (1966) context simply in terms of absolute number of species present.

Whether their analysis in the context of hypotheses on stability-time-disturbance of the benthic marine communities is desirable (Sanders, 1969; Slobodkin and Sanders, 1969; Dayton and Hessler, 1972; Connell, 1978), certain demersal fish assemblages in the seas adjacent to the South China Sea have been shown to be undergoing a significant temporal-spatial change in structure resulting from disruptions through overfishing (Pope, 1979; Pauly, 1979, 1982; Gulland, 1987; McKenna and Saila, 1991). Adjacent to the Gulf of Papua, Poiner and Harris (1986) also noted such a change due to the impact of commercial prawn trawling in the Gulf of Carpentaria, Australia. The demersal fish fauna of the Papuan Gulf is similar to those Indo-Pacific fish systems in structure (Harris and Poiner, 1990) and, perhaps, in function as well (Rainer, 1984), with the ubiquitous leiognathids plus carangids and sciaenids plus pomadasyids and mullids as, respectively, the major nektonobenthic and benthonektonic components. Therefore, its stability is expected to be vulnerable under any heavy exploitations that

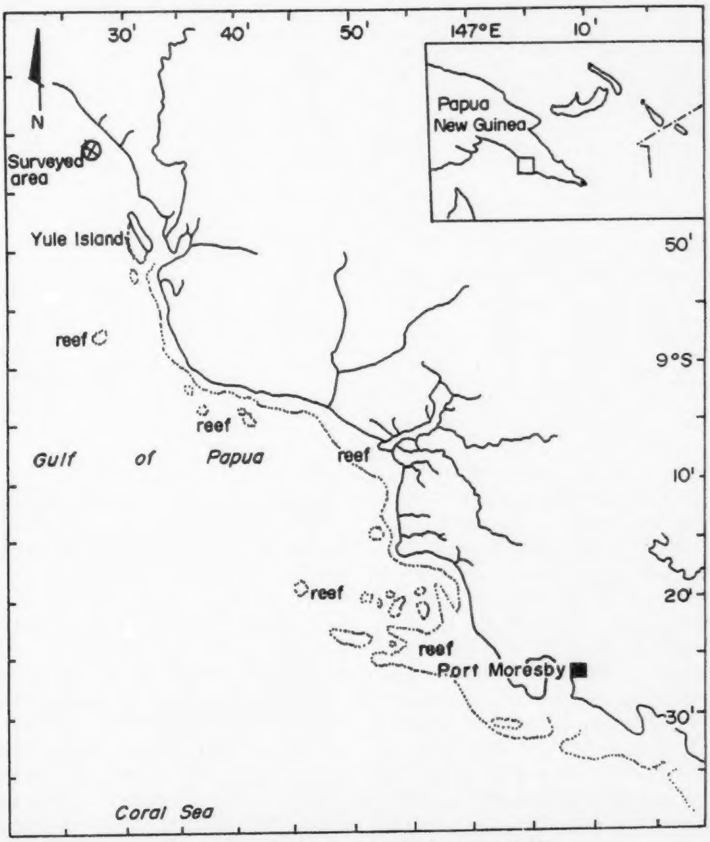

Figure 1B. — Study area in the Gulf of Papua, PNG.

may result in a vastly declining fishery production (Pope, 1979; Pauly, 1979, 1982; Poiner and Harris, 1986; Lowe-McConnell, 1987).

Current fishing intensity in the Gulf of Papua is considered moderate, if not low, being exerted mainly on the stocks of prawn and lobster (DFMR, 1989) and, occasionally, shark (Chapau and Opnai, 1986). However, fishing pressure on the Gulf demersal fish communities may grow considerably in view of a policy (DFMR, 1989; Agrodev, 1991) adopted recently by PNG to vigorously develop its fishery resources, aimed at a substitution of imports of the canned mackerels (up to US$50 million per year; Olson and Kan[2]). Previous relevant data only deal with the northwestern portions of the Gulf (Liem and Haines, 1977; Kailola and Wilson, 1978; Roberts, 1978; Watson, 1984). Along with the present findings from a northeastern Gulf fish assemblage, these data provide baseline information for the planning of fisheries development in the Gulf of Papua.

Table 3.—Comparison of catches (kg) under two TED trawling conditions.

Year(s)	Taxocene	TED-closed/TED-open: No. of trawls	Total weight	Range	Mean	S.D.	Retention ratio (%)[1]
1988–89	Penaeids	13/13	81.8/72.2	2.8–10.9/1.7–10.9	6.3/6.6	2.7/2.3	88.9
	Leiognathids	13/13	291.0/305.0	3.5–65.6/4.2–45.9	22.4/23.5	17.6/15.1	105.0
	Pomadasyids	13/13	247.0/59.5	2.1–32.4/1.0–12.8	19.0/4.6	8.5/3.2	24.2
	Polynemids	13/13	48.2/13.2	0.1–19.4/nil–5.0	3.7/1.0	5.0/1.4	27.0
	Sciaenids	13/13	43.1/14.4	nil–15.0/nil–5.0	3.3/1.1	4.4/1.5	33.3
	L. lactarius	13/13	37.4/28.0	0.1–16.9/nil–7.9	2.9/2.2	3.9/2.6	75.9
	Other fishes	13/13	107.0/55.9	3.8–12.5/1.0–12.9	8.3/4.3	3.0/2.9	51.8
	Mean		129.0/79.4	1.5–27.0/1.0–14.9	9.9/6.1	7.1/4.5	61.6
1990	Penaeids	7/6	38.3/32.2	3.5–7.5/2.8–10.2	5.5/5.4	2.1/2.7	98.2
	Leiognathids	7/6	229.0/118.0	10.4–68.8/8.5–39.9	32.8/19.7	21.8/19.7	60.1
	Pomadasyids	7/6	163.0/15.2	7.0–45.6/0.5–6.0	23.4/2.5	16.2/2.1	10.7
	Polynemids	7/6	113.0/12.6	3.8–40.8/0.5–4.4	16.2/2.1	12.0/1.3	13.0
	Sciaenids	7/6	43.0/18.6	2.1–9.4/0.5–5.5	6.1/3.1	2.3/1.9	50.8
	L. lactarius	7/6	143.0/102.0	10.0–30.0/3.8–36.5	20.7/17.0	7.5/11.5	82.1
	Other fishes	7/6	16.0/9.7	nil–3.0/nil–2.2	2.3/1.6	1.1/0.9	69.6
	Mean		118.0/46.0	5.6–32.9/2.3–15.8	16.9/7.7	10.2/5.0	45.6

[1] Note: Retention ratio is calculated from mean (open)/mean (closed) × 100.

Table 4.—Comparison of difference in catch weight (kg) under two TED trawling conditions. Note: F test of variance is at a 90% level of significance. Sign in the parentheses indicates a significant difference. The asterisk (*) indicates a significant difference at the 90% level.

Taxocene	Variance: TED closed	Variance: TED open	F-value	Mean: TED closed	Mean: TED open	t-value
Between the two TED conditions for 1988–89 (13 pairs)						
Penaeids	7.4	5.4	1.37(–)	6.3	5.6	0.72(–)
Leiognathids	309.0	228.0	1.35(–)	22.4	23.5	0.17(–)
Pomadasyids	72.9	9.9	7.35(+)	19.0	4.6	5.45(+)
Polynemids	24.9	2.3	12.28(+)	3.7	1.0	1.80(–)*
Sciaenids	15.2	2.2	6.79(+)	3.3	1.1	1.88(–)*
L. lactarius	19.4	7.0	2.78(+)	2.9	2.2	0.51(–)
Other fishes	9.9	8.6	1.04(–)	8.3	4.3	3.28(+)

Taxocene	Variance: 1988–89	Variance: 1990	F-value	Mean: 1988–89	Mean: 1990	t-value
Between years under the TED-closed condition (13 sets vs. 7 sets)						
Penaeids	7.4	4.4	1.73(–)	6.3	5.5	0.69(–)
Leiognathids	309.0	475.0	1.53(–)	22.4	32.8	1.16(–)
Pomadasyids	72.9	262.0	3.60(+)	19.0	23.4	0.81(–)
Polynemids	24.9	144.0	5.78(+)	3.7	16.2	3.31(+)
Sciaenids	15.2	5.3	3.60(–)	3.3	6.1	1.81(–)*
L. lactarius	19.4	56.3	3.66(+)	2.9	20.5	6.84(+)
Other fishes	9.9	1.2	7.76(+)	8.3	2.3	5.06(+)

Performance of Our TED Gear

Manifestation of this assemblage in the present catches is significant. As an estuarine species associated with low salinities (<5‰) in PNG (Quinn and Kojis, 1986), *L. lactarius* was very common in April during 1989–90 but was extremely rare in the same month in 1991 (Tables 2, 3). The reverse was true for *Arius armiger*, a marine fish, with 11 congenerics occurring in two river systems in the Papuan Gulf (Berra et al., 1975; Roberts, 1978) and the Sepik River in northern PNG (Allen and Coates, 1990). Both cases resulted from an inflow of oceanic waters, as we have observed. This is also reflected in catch composition and weights in our assessment of the TED-open gear in terms of its potential to reduce finfish bycatch (Tables 3, 4).

Our data indicate that, while being trawled, the TED-open net is able to retain prawns (retention ratio 89–98%) and to exclude finfish, though to a highly variable fashion (11–100%, mean 46%) (Table 3). This performance is similar to that of three types of TED-equipped gear tested in the Gulf of Mexico: 95–97% for prawn retention and 11–88% for finfish exclusion (Watson et al., 1986) and, perhaps, to that of the separator gears tested off Scotland as well (Main and Sangster, 1982). The wide variation observed by us in finfish exclusion was caused by different responses to the dual trawling condition between the nektonobenthic leiognathids and *L. lactarius* and the benthonektonic groups., e.g. pomadasyids, polynemids, and sciaenids. These results have demonstrated that the TED-open type of gear is capable of harvesting the prawn while conserving demersal fish. Also, as noted by Matsuoka and Kan (1991), this gear has only a moderate negative trawling impact on smaller demersal fish except perhaps the pomadasyids.

For general use, two variables, F_c and F_o, in the formula proposed for the measurement of the TED gear performance, E (Kan et al., 1989; Matsuoka and Kan, 1991), should be redefined to cover all trawlable nekton concerned including the *Loligo* cephalopods, a prominent

[2] Olson, F. L., and T. T. Kan. 1989. The fishery resources of Papua New Guinea. Univ. PNG, Dep. Fish., Port Moresby, Unpubl. rep., 21 p.

component of several Indo-Pacific, often heavily exploited, bottom fish and prawn systems (Longhurst and Pauly, 1987; Gray, et al., 1990; Harris and Poiner, 1990; Shaw et al., 1990; McKenna and Saila, 1991). This measure is now proposed as follows:

$$E(\%) = \frac{N_c - N_o}{N_c} \times \frac{P_o}{P_c} \times 100 \qquad (5)$$

where N_c is the catch weight of all nekton other than prawn in the TED-closed or control net, N_o, the catch weight of all nonprawn nekton in the TED-open or test net, P_c, the catch weight of prawns in the TED-closed or control net, and, P_o, the catch weight of prawns in the TED-open or test net. Theoretical consideration of this measure, E (%), is that the performance of any TED or similarly equipped gears should be judged by the extent expressed in their dual function: to exclude all nonprawn nekton and to retain the prawns. Performance here varies from zero (N_c = N_o and/or P_o = 0) to full (N_o = 0 and P_c = P_o) effectiveness.

Temporal-spatial variability of E should be great due to various abiotic, biotic, and human factors interacted in an assemblage of bottomfish ground. The value of E in this study was greater in 1990 (51%) than 1988–89 (34%) owing to an interyear fluctuation of abundance (biomass) of leiognathids and *L. lactarius* (Table 3). Compared to 1988–89, the relative abundance of this species was negligible in April 1991 when salinity was high (Table 1). Whether or not the abundance (biomass) of prawns affects E, it certainly does affect the weight of bycatch. Prawning fleets in the Gulf of Papua and Torres Strait expend effort differently over time and space (Kolkolo, 1983; Williams, 1986), apparently responding indirectly to the effect of higher salinities which are caused by the interactions of winds, currents, river runoffs and plumes, and topographic features (Wolanski et al., 1984). Unfortunately, our data on any links among salinity, prawn biomass, and finfish catch weights are inconclusive (Matsuoka et al., 1991). Further trials should be conducted for the typical "Lahara" and "Laurabada" types of fish/nekton assemblages.

Our TED-open net has shown an average E of 43%, calculated from the catch results between 1988 and 1990. Based on data of an earlier test of a variety of TED gears conducted off Mississippi-Louisiana (Seidel, 1975), their average E, calculated by us, was 27%. The E later advanced to 41% (Watson and McVea, 1977) and > 50% (Watson et al., 1986) with several improved versions of TED gears tested there. All of these results, including ours, have pointed out that most, if not all, TED/separator-equipped prawning gears are able to retain the prawn (target catch) effectively and to exclude the finfish (bycatch) ineffectively. Many fishes, e.g. ariids, stromateids, and sciaenids, were well excluded by two recent TED gears in the Gulf of Mexico (Watson et al., 1986). If only demersal fish were treated, the E during 1988–90 in our study could be as high as 65%. Apparently, the two 40 x 40 cm side windows of our TED have facilitated escapement for the demersal component of the present taxocene (pomadasyids, sciaenids, and polynemids).

Behavior of the Fish and Prawn in Relation to Escapement

The prawn component of the above formula for E, P_o/P_c, remains large in all relevant data available for calculation by us, ranging from 0.70 (Seidel, 1975), to 0.78 (Watson and McVea, 1977), 0.88 (Matsuoka and Kan, 1991), 0.92 in this study, and 0.95–0.97 (Watson et al., 1986). These results support a general observation that prawns are weak swimmers with little directional avoidance when stimulated either by the currents in natural water (Quinn and Kojis, 1987) or netting (Ko et al., 1970; Seidel, 1975; Watson, 1976; Valdemarsen, 1989). Prawn behavior thus directs the gear technologists away from paying attention to possible responses of the prawns in their design of high performance (E) separator/TED-equipped gears, except for a task of designing the gears on prawn size selectivity in terms of stock conservation.

Fish behavior and its use in capture fisheries has been recognized by biologists and gear technologists (Bardach et al., 1980; Wardle, 1983, 1986). Chen et al. (1989) reported an effect of mesh size on trawling and trawl fishes in relation to their escapement via different parts of an experimental gear. Watson (1989) presented an excellent discussion on the behavior of trawl fish and prawn in the Gulf of Mexico with proposals on modifications to prawn trawl design which may greatly reduce the finfish bycatch associated with a penaeid prawn fishery.

One of the TED gears of the J. W. Watson team, with a device which acts as a mechanical stimulus for fish avoidance and escapement, has achieved a finfish separation rate up to 80% with no significant loss of prawn in catches (Watson et al., 1986). This level of effectiveness is the minimum deemed acceptable by the PNG prawn industry in terms of TED gear feasibility in commercial prawning (Matsuoka and Kan, 1991). Our results only yield an effectiveness (E) about 51%. Here, the biological difference has been small among the component of benthonektonic fish whether it is observed from the Gulf of Papua, the Gulf of Mexico, or the North Sea (Main and Sangster, 1982).

Three highly TED-excludable fishes in our study, pomadasyids, polynemids, and sciaenids, are swift carangiform or subcarangiform type swimmers (Webb, 1975). Their body and tail shapes would give them the typical caudal fin aspect ratio (A) (Pauly, 1989a) of demersal fish of around 1.5 (Pauly, 1989b; Sambilay, 1990) and, while swimming, moderate Reynolds numbers, from R_e>5×10^3 to R_e>5×10^5 (Aleyev, 1977). These figures indicate their "burst" rather than "sustained" swimming mode. The functional morphology of the soft rays in these fish and many of their counterparts in the Gulf of Mexico and North Sea also signals their capacity for thrusting and maneuvering (Arita, 1971). Both the swimbladder and lateral line system are well developed, especially in the sciaenids. Specialized sensory structures for probing and tasting are frequently featured in the form of mandibular barbels (sciaenids and pomadasyids), pores on snout and lower jaw (sciaenids), and gustatory buds on free rays (polynemids) (Atema, 1980). It is considered

that these benthonekton are sensitive and versatile and, therefore, highly adaptive as well as adjustable to any environmental changes either natural or caused by humans. They should be able to avoid an approaching net or escape from it via any exits available, e.g. a TED.

In night trawls off Mississippi and Alabama during mid-August to late September 1984, a collapsible fiberglass TED gear achieved very high reduction rates of 69–100% for three schooling neritic/epipelagic fishes: *Brevoortia patronus*, *Harengula jaguana*, *Scomberzomorus maculatus* (Watson et al., 1986). Our selective gear was extremely poor in excluding several carangiform swimmers including *L. lactarius* and especially leiognathids (Tables 2, 3, 4). This contrast may be due to certain faunal differences in test grounds between the Gulf of Mexico (lat. 30°N) and the Gulf of Papua (lat. 9°S). However, the above TED gear, while being tested, appeared to have disengaged any dense fish schools. Schoolers, especially the small pelagic/neritic clupeiformes and probably carangiformes, tend to break up from the compact schools at night (Hara, 1985; Thomas and Schulein, 1988). Kemmerer (1980) gave evidence of a disintegration at night of *B. partonus* schools in the northern Gulf of Mexico. Major schools of *S. maculatus* off Alabama and Mississippi might have already migrated eastward to the Florida coasts or westward along the Mexican coasts before mid-August (Collette and Nauen, 1983; Longhurst and Pauly, 1987). We are unaware of any valid data on the diel variation among schooling species in prawn bycatches observed in PNG or Queensland waters (Gray et al., 1990). However, calculated by us from R. A. Watson's (1984) data, the diel variation of average bycatch weights of the leiognathids in PNG commercial trawls is great indeed: 130 kg/day-trawl vs. 17 kg/night-trawl. Therefore, as is also true in sampling a nonreef demersal fish/nekton assemblage (Allen and DeMartini, 1983; DeMartini and Allen, 1984; Quinn and Kojis, 1987), any tests on the effectiveness of selective gears should be compared between day and night, especially if a component of schooling species is known to be large in an assemblage or a bottom fish ground concerned.

Ubiquity of the leiognathids has been well appreciated in several Indo-Pacific fish assemblages, in Singapore, Hong Kong, and PNG (Chua, 1973; Richards and Wu, 1985; Quinn and Kojis, 1986), and numerous prawn trawls in the Papuan Gulf and Torres Strait (Watson, 1984; Harris and Poiner, 1990). In probably every single haul in the present study, *L. splendens* and *Secutor ruconius* occurred the most in both weight and number (Tables 2, 3; Matsuoka and Kan, 1991). Meanwhile, Pinto (1988) noted for *L. brevirostris* and *S. ruconius* the two highest in total mortality, *Z*, among many fishes in a bay community in the Philippines.

Some aspects of reproduction of the leiognathids have been observed in the seas around southern India (Arora, 1951; Balan, 1963; James, 1975; James and Badrudeen, 1975; Murty, 1983). In general, these schooling silverbellied fish live neritic/nektonobenthic lives of <3 years, attain maturity around age 0–1 at 60–70 mm (a size similar to the peak length class we here observed; Matsuoka and Kan, 1991), and spawn more than once per year as either regular or opportunistic spawners with a high absolute fecundity, relative to their body size, of between 8,000 and 12,000 eggs. Their *Caranx*-like body shape should give an aspect ratio (*A*) about 4 (Palomares and Pauly, 1989; Pauly, 1989b) and a Reynolds number, $R_e>10^5$ (Aleyev, 1977), rendering them of a swimming mode more "sustained" than "burst," as favored in the maintenance of compact schools as "operational structures" (Breder, 1976).

Seigel (1982) described a locking mechanism of median fin spines in leiognathids, suggesting functions in defense and metabolic advantage via fin erection and, possibly, sound production. These functions would primarily benefit nonschooling and/or bottom fishes. We therefore interpret this mechanism as being adaptive to the schooling and surface/subsurface leiognathids in that, when simultaneously locked by all members in a school, it would help reduce the energy required to maintain uniformity and fluidity of schools while cruising (Breder, 1976). This would be similar in functions to automatic "cruise (speed) controls" frequently used in modern airplanes in the open sky and even automobiles on the open expressways for precise and easy cruising. The leiognathids' secretion of the thick mucus layer over the skin is also significant in sustaining their schooling efficiency while cruising (Breder, 1976). This ability to secrete, along with a highly protrusible mouth to facilitate feeding (Schaffer and Rosen, 1961) and other features mentioned above, has adapted the 25 or so carnivorous and bacterially bioluminescent leiognathid species extremely well to coastal, bay, and estuarine (Chua, 1973) environments throughout the Indo-West Pacific (James, 1975; Dunlap and McFall-Ngai, 1984; Shen and Lin, 1985). Whether or not directly contributed by a schooling behavior alone, leiognathid abundance or success has been a consequence of interplay between adaptation and evolution of the fishes concerned (eventually, "r-strategist"; Pianka, 1978) since probably the Oligocene-Miocene (Romer, 1966). Ironically, as illustrated by Murphy (1980), modern time fishing operations nearly negate all adaptive advantages of fish schools (Breder, 1976; Patridge, 1982) including those of the present leiognathids.

Balan (1963) stated that the surface or subsurface *L. bindus* schools moved toward the top film of waters upon fishing. Chen et al. (1989) indicated that the schooling *L. brevirostris* and *Setipinna taty* tend to swim upward at netting. From the profile of caught animals in nets, we noted the leiognathids usually on top. Therefore, some selectivity may be possible by modifying the net design and trawl configuration. For example, a low and canopied net opening which is made mechanically to open only near or on the bottom should reduce the quantity of leiognathids and other ecologically similar fish entering the trawl. Also, configuration and length of the filter or funnel and main nets of a gear may be modified to reduce the escapement of underutilized demersal fish (Workman and Taylor, 1989) or to enhance, as suggested by Matsuoka and Kan (1991), that of the ubiquitous sur-

face fish, or somewhat to achieve both (Chen et al., 1989). Further, night trawling may encounter fewer fish schools composed mainly of bycatch species in the Gulf of Papua.

Bycatch and Its Impacts on PNG Fisheries Development

Despite their small body size, the leiognathids support commercially important fisheries in southern India (James and Badrudeen, 1975). As bycatch or target catch from the multispecies fisheries, the leiognathids along with ecologically similar fish are processed and marketed extensively in the southeast Asian region (Suwanrangsi, 1986; Ng and Hooi, 1987; Jean and Kuo, 1988). By contrast, finfish bycatch is almost totally wasted in the PNG prawn fishery; Watson (1984) estimated that only 250 t of primarily large fish were retained for sale fresh in 1982, and Agrodev (1991) recorded such a weight of 450 t in 1989. Bycatch discard has the effect of transferring large quantities of biological material from the bottom to the surface (Hill and Wassenberg, 1990). Bycatch discards benefit a few opportunistic scavengers and predators at or below the surface, as we and Hill and Wassenberg (1990) have observed, and on the bottom. The ecological efficiency in this transfer process initiated by trawlers must be extremely low. In terms of economic considerations on operational costs (gear, vessel, fuel, crew time, etc.) and harvest quality/value (less damaged prawns), current prawning economics in the Gulf of Papua should be considered greatly improvable using selective gears such as one TED equipped. The TED gear used in this study needs to be further evaluated, along with a bioeconomic analysis to identify its potential ecological and operational benefits. Nevertheless, to deal with the bycatch problem in prawn fisheries in regions such as the Gulf of Papua and Torres Strait, a strategy of bycatch reduction is more prudent than that of bycatch utilization (Pender and Willing, 1989).

Suggestions for various uses of the prawn bycatch for farm animal (e.g. crocodile) feeds and human consumption in PNG have been made from biological (Watson, 1984; Dalzell, 1986) and some bioeconomic (Witcombe, 1978; Barratt, 1986; Rajeswaran[3]) points of view. These uses may be ecologically and technologically attainable at both appropriate technology (Reilly and Barlie, 1986; NRC, 1988) and institutional (Okada et al., 1988) scales. However, it is highly doubtful that these uses, suggested for human consumption via commodities (Barratt, 1986), are socioeconomically viable in view of the consumption pattern of fishery products prevailing in PNG. PNG determined in 1986 (Kan and Hill, 1988) to develop its tuna fishery and other marine resources that are extremely rich in size and variety and readily retrievable as well as marketable worldwide (Philipson, 1989). Ironically, this country has become a world leader in canned mackerel imports, on average 25,000 t at US$24 million per year between 1980 and 1986 (Olson and Kan[2]). From 1982 to 1989, while the market weight of prawn finfish bycatch increased from 250 t to only 450 t, the imports of canned mackerel had tripled from 10,900 t to 33,000 t (Agrodev, 1991). Massive influx of this single import item is creating a "tinpis"[4] phenomenon in PNG; it appears to have already been a major socioeconomic constraint to the planning and development of fisheries and aquaculture (Kan, 1986) in PNG as well as in several other developing countries in this region (Lawson, 1978).

FAO-IDRC (1982), Saila (1983), and Alverson et al. (1994) drew attention to the wasteful disposal of trawl bycatches worldwide. Watson (1989) summarized the development of separator-equipped gears in trials conducted in the North Pacific, the North Atlantic, and especially the Gulf of Mexico from the late 1960's. Unfortunately, the concept of this type of gear in finfish bycatch reduction for ecological and economic benefits has been given insufficient attention by fisheries managers and gear technologists in the entire Indo-West Pacific region except of those from Indonesia and Australia (Sujastani, 1984; Mounsey[5]). This may result from a difference in the use pattern of various fishes, e.g. the leiognathids, as bycatch in the Gulf of Papua but as catch or even target catch in the south and southeast Asian regions. Nevertheless, the gear we studied is effective in excluding the demersal fishes while retaining the prawns. It, or a modified version of it, could be tested on a large commercial or intermediate technology scale. It is inexpensive, simple, and foldable; hence, it could also be used at a small subsistence or appropriate technology level (Cook and Tenakanai, 1986; NRC, 1988). Meanwhile, it ought to be an ideal sampler in the study of fish behavior and gear selectivity, especially employed along with the general type (Gibbs and Matthews 1981–2) or special type (Chen et al., 1989; Workman and Taylor, 1989) of samplers. This multipurpose gear is also extremely simple.

A balance between ecological and economic benefits must be sought in the use of modern fishing gears. Unlike probably the drift net and, to a certain degree, the modern purse seine, these gears should be highly selective. The future of fisheries management is managing the fisherman (Larkin, 1988) and his gears, whether in a developed or developing country or region.

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[3] Rajeswaran, N. 1990. Small scale fish meal processing in Papua New Guinea. Dep. Fish. Mar. Resour., Resour. Develop. Enforce. Br., Port Moresby, Unpubl. rep., 15 p.

[4] "Tinpis" is the PNG Pidgin English word for any processed and merchandized fish, especially mackerel in cans.

[5] Richard Mounsey, Senior Fishing Gear Technologist, Department of Primary Industry and Fisheries, G.P.O. Box 990, Darwin, N. T. 0801, Australia. Personal commun., July 1993.

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Australian Vessel Performance in the East Coast Tuna Longline Fishery

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Introduction

The Australian east coast tuna longline fishery is currently exploited by domestic vessels and by Japanese vessels under an access agreement. The Japanese fleet access to eastern Australian waters is shown in Figure 1. About 100 Japanese vessels were involved in 1989, although numbers have since fallen to around half that level. Their fleet consists of three groups of vessels: large (200–500 Gross Registered Ton, GRT) longliners which fish in the southern part of the Japanese fishery (south of lat. 25°S) when the southern bluefin tuna, *Thunnus thynnus,* fishery is not underway; smaller (150–200 GRT) longliners which fish in Australia's northern tropical and subtropical waters and in the adjacent Exclusive Economic Zones (EEZs); and a small group of Japanese vessels which follow the stocks in both the northern and southern zones of the fishery. The Japanese vessels target the full range of tuna and billfish species available in the Australian EEZ, the total catch being 6,068 metric tons (t) on average in the years 1987–89. The average catch composition by weight was: 2,589 t yellowfin tuna, *Thunnus albacares* (about 43% of the total by weight), 557 t bigeye tuna, *Thunnus obesus* (9%), 1,453 t albacore, *Thunnus alalunga* (24%), 699 t swordfish, *Xiphias gladius* (11.5 %), and 770 t marlin (12.5%) (148 t black marlin, *Makaira indica*, 281 t blue marlin, *Makaira mazara,* and 341 t striped marlin, *Tetrapturus audax*) (McIlgorm, 1995).

The Australian vessels operate from various ports along the coast. They are typically smaller (<15 m) than the Japanese vessels, operate with lighter monofilament gear than the Kuralon[1] used by the Japanese, and target stocks which are closer to the surface. Of the approximately 100 Australian boats engaged in the fishery, 50% reported catching only yellowfin tuna. The catch composition by weight of the Australian fleet during 1987–89 averaged 295 t yellowfin tuna (85%), 9 t bigeye tuna (3%), 31 t albacore (9%), 5 t swordfish (1%), and 7 t striped marlin (2%) (McIlgorm, 1995). The overwhelming concentration of yellowfin tuna in the Australian vessels' catch, as compared with the Japanese vessels, is explained by the tendency of Australian vessels to fish surface schools within 50 n.mi. from shore (Fig. 2). For this reason, the Australian fishery, unlike the Japanese fishery, can be modeled as a single-species fishery, with catches of other species regarded as by-catch. An analysis of the performance of the multispecies Japanese vessels is contained in McIlgorm (1995).

This paper describes the results of an analysis of the catching performance of the Australian vessels in the fishery. A sample of 3,860 daily observations on domestic vessels engaged in the fishery in the period 1987–90 was used to relate tuna catch to vessel characteristics and operations. The effect on the catch of factors such as vessel type, fishing conditions (moon phase, sea surface temperature), fishing practices (soak time, patrolling the longline), location in terms of distance from the coast, and seasonal and annual fluctuations in stocks is estimated.

Tuna Production Model

The basis of the analysis is the Cobb-Douglas production function which is a simple economic model of production which describes the harvesting of tuna by an individual vessel:

$$h = AE^{\alpha}x^{\beta},$$

where h is daily harvest in metric tons, E is the daily amount of effort measured in thousands of hooks fished, x is the stock of tuna susceptible to the vessel's fishing gear during the day, A is the catchability coefficient, and α and β are constants. A special form of this model, in which $\alpha = \beta = 1$, was adopted by Schaefer (1967) in a time-series study

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ABSTRACT—A sample of daily observations on the activities of Australian vessels longlining for yellowfin tuna, Thunnus albacares, *during 1987–90 was analyzed, using a production function approach, to determine the effects of vessel characteristics and operational practices and conditions. Significant differences were found between the tuna fisheries in the northern and southern regions of the inshore yellowfin tuna fishery in the east Australian Exclusive Economic Zone. The type of vessel used, and fishing practices such as soaktime, patrolling the longline, and choice of surface water temperature were found to have significant effects on yellowfin tuna catch rates.*

[1] Mention of trade names or commercial firms does not imply endorsement by the National Marine Fisheries Service, NOAA.

of the eastern Pacific yellowfin tuna fishery, and it has been extensively used in bioeconomic studies to relate total harvest to fishing effort and fish stock. The model has also been used in cross-sectional studies to estimate the relationship between the catch and effort of individual vessels. Examples are the Strand et al. (1981) study of the Atlantic surf clam fishery, and the Bjorndal (1989) study of the North sea herring fishery. Other cross-sectional studies, such as those of Morey (1986) and Squires (1987), estimate cost functions derived from general forms of production functions which include the Cobb-Douglas as a special case.

The Cobb-Douglas production function cannot be directly estimated because of the absence of observations on the stock of fish encountered by each vessel. For this reason it will not be possible to estimate the catchability coefficient, A, or the coefficient of stock, β. However, indirect measures of the factors influencing catchability, and of stock levels, can be generated by means of a series of dummy variables. Using these measures, together with the observations on catch and effort, the constant, α, on fishing effort in the production function can be estimated. The factors affecting the tuna stock encountered by each vessel, and the vessel's catchability coefficient can be divided into the categories of vessel characteristics, fishing practices, and stock levels.

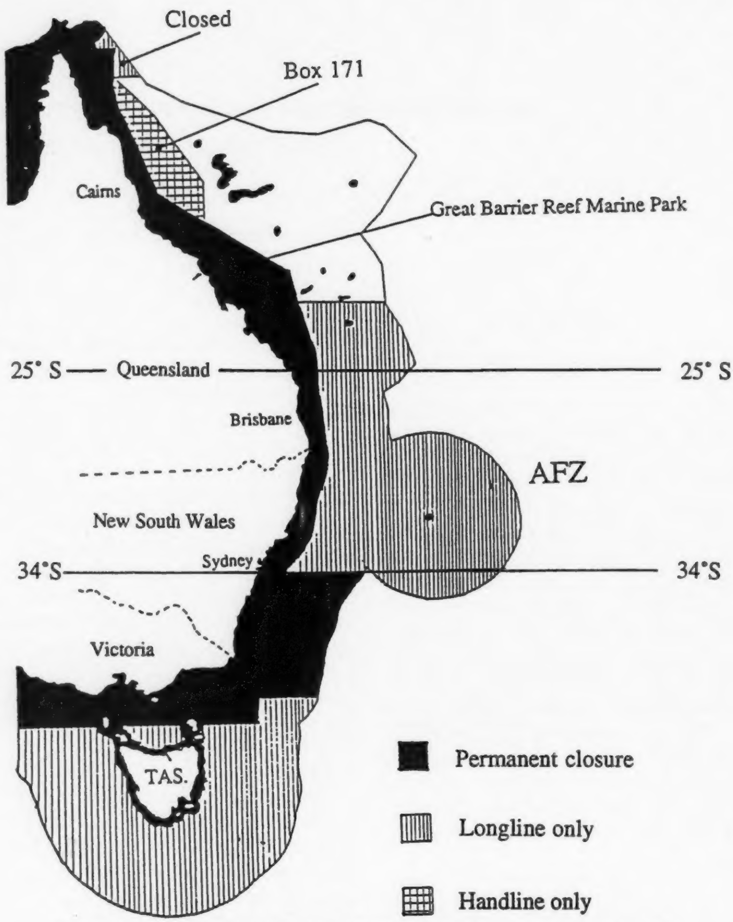

Figure 1. — Japanese vessel access to the east Australia Fishing Zone (AFZ) in 1989. The areas south of lat. 34°S, adjacent to the Great Barrier Reef Marine Park and Box "171" have been closed to fishing since 1984.

Vessel Characteristics

Four types of vessels are used in the domestic longline fishery. Planing longliners are high-speed, high-horse power, low-displacement hull vessels of up to 15 m length and are commonly used in Australian rock lobster fisheries. Multipurpose vessels are displacement-hull vessels under 15 m that undertake alternative fisheries such as trapping, droplining, or potting, as well as tuna longlining. Many trawlers convert to longline gear when the tuna stocks are available, whereas purpose-built longliners are displacement-hull vessels that can be up to 18 m in length and have been designed specifically for longlining and droplining of fish for fresh markets. It is possible that the vessels which are specifically designed for the fishery will have an advantage in terms of catchability, and that the speed of the planing longliner and the length of purpose-built vessels will provide an additional advantage.

Fishing Practices

Several choices which are made by vessels may affect catchability and/or the level of stock open to exploitation. Catchability may be affected by the length of soak time, by intermittent patrolling of the longline during the day to retrieve fish and rebait hooks, or by moon phase. Catchability is thought to rise in the darker phases of the moon (DPIE[2]), and tidal patterns are also associated with moon phase. The choice of where to fish in terms of distance from the coast (0–12, 12–50, 50–100, or >100 n.mi.), or in terms of sea surface temperature may affect the stock level in the locality.

[2] DPIE. 1990. New South Wales logbook coordinators report. Aust. Fish. Serv., Dep. Primary Ind. Energy, Canberra, Aust. Unpubl. doc.

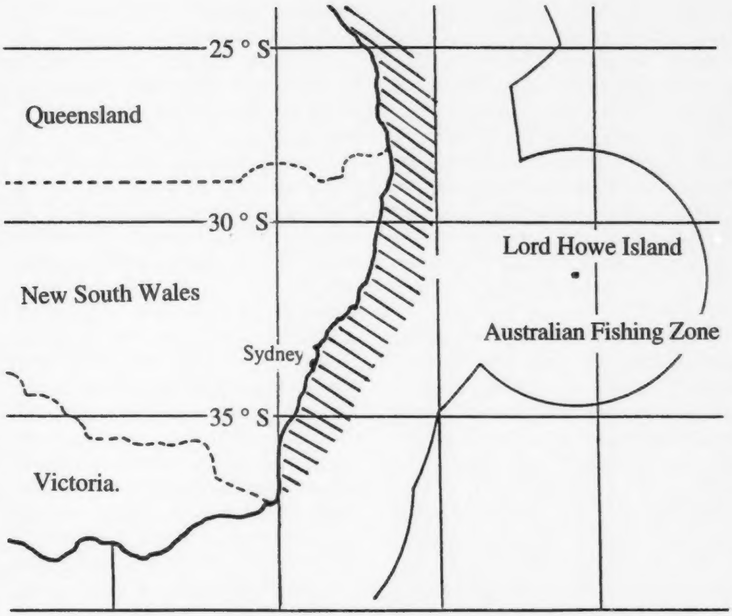

Figure 2. — The area of the domestic fishing effort along the New South Wales and Southern Queensland coasts. The hatched area represents the inshore fishing grounds favored by the domestic vessels.

Stock Levels

Harvest will be determined by the level of fish stocks susceptible to the vessel's fishing gear during the day, the latter being influenced by the general stock conditions in the EEZ. Tuna and billfish are migratory, and stocks are known to fluctuate on a seasonal and annual basis.

All these factors are accounted for in the production analysis. In addition the analysis allows for the possibility of significant differences between the northern and southern zones of the domestic fishery. The northern zone is defined as the area north of Sydney, from lat. 34° to 25°S; the southern zone is the area south of Sydney, from lat. 34° to 38°S (Fig 2).

Estimation

It is convenient to estimate the production model in logarithmic form. The equation estimated is:

$$\ln(h) = A + aPt + b_1Z_1 + b_2Z_2 + b_3Z_3 + c_1C_1 + c_2C_2 + c_3C_3 + m_1M_1 + m_2M_2 + m_3M_3 + q_1Q_1 + q_2Q_2 + q_3Q_3 + y_1Y_1 + y_2Y_2 + y_3Y_3 + \alpha\ln(E) + \gamma T + \delta\ln(St) + U,$$

where: $\ln(h)$ is the natural logarithm of daily yellowfin tuna harvest, A is a constant, a, b_1, b_2, b_3, c_1, c_2, c_3, m_1, m_2, m_3, q_1, q_2, q_3, y_1, y_2, y_3, α, γ, and δ are coefficients to be estimated, Pt is a dummy variable taking the value 1 if the longline was patrolled and zero otherwise, Z_1, Z_2, and Z_3 are dummy variables representing the 12–50, 50–100, and >100 n.mi. zones from the coast (with the default value of the dummy representing the 0–12 n.mi. zone), C_1, C_2, and C_3 are dummy variables representing the vessel classes multipurpose vessels, trawlers, and purpose built vessels, respectively (with the default value of the dummy representing planing longliners), M_1, M_2, and M_3 are dummy variables representing the new moon, first quarter, and full moon respectively (with the default value of the dummy representing the last quarter), Q_1, Q_2, and Q_3 are dummy variables representing the April–June, July–September, and October–December quarters, respectively (with the default value of the dummy representing the January–March quarter), Y_1, Y_2, and Y_3 are dummy variables representing the years 1988, 1989, and 1990, respectively (with the default value of the dummy representing 1987), $\ln(E)$ is the natural logarithm of the number of hooks fished in the day, T is a temperature-related variable which measures stock availability, and St represents soak time and U is a random error term assumed to have zero mean and constant variance.

The Australian vessels primarily harvest yellowfin tuna. Researchers have determined upper and lower bounds for water temperatures where they are known to range, and fishermen search for a level of sea surface temperature (SST) which they believe maximizes the chance of locating fish. In this study, the optimum water temperature was assumed to be 21.5°C. If yellowfin tuna stocks tend to be most abundant in waters of 21.5°C, then it can be assumed that the further the actual SST is from this value, the lower the stock level. A crude indicator of the stock level available to a vessel is given by $1/\exp(\gamma T)$ where T is the absolute value of the difference between the actual SST and the optimal temperature. If a vessel is fishing waters at 21.5°C the stock indicator takes on a value of unity; this value declines exponentially as the water temperature diverges from the optimum. Since the larger the value of T the lower is the stock assumed to be in the vicinity of the vessel, it would be expected that the estimated value of γ, the coefficient on T, would be negative.

The equation is first estimated by Ordinary Least Squares (OLS) using all the observations in the sample. Tests indicated the presence of heteroscedasticity in the sample, and standard data transformations were performed in an unsuccessful attempt to eliminate this problem. In the presence of heteroscedasticity in the sample, the OLS coefficient estimators are unbiased but the estimated t statistics are biased. The sample is then divided into northern and southern subsamples, and a log likelihood radio test is used to determine whether the production processes in the north and south are the same. This test indicated that the northern and southern zones should be regarded as distinct fisheries. The northern and southern

samples were then examined to determine whether any groups of variables could be excluded as having an insignificant effect on yellowfin tuna catch. It was found that in the northern fishery, yellowfin tuna catch did not vary significantly with distance from shore, and this set of variables was dropped from the model. In the southern fishery, it was found that yellowfin tuna catch was not significantly affected by distance from shore, vessel class, or moon phase, and these variables were dropped from the model.

Results

Since the northern and southern fisheries were found to have different characteristics, results will be reported for each. Table 1 reports the coefficients estimated for each of the independent variables in final versions of the estimating equations, together with t statistics. Coefficient estimates which are significantly different from zero at the 1%, 5%, and 10% levels of significance are marked by asterisks. As mentioned above, these tests of significance may not be reliable because of the problem of heteroscedasticity.

Discussion

In the initial estimations it was found that moonphase and class of vessel had no significant effect on yellowfin tuna catch in the southern fishery, and these variables were omitted from the final specification of the southern model. Patrolling the longline was found to have no significant effect on yellowfin tuna catch in the northern fishery and this variable was also omitted. Distance from shore was found to be significant in neither fishery, suggesting that performance is influenced by local availability of fish rather than choice of fishing ground.

The coefficients on the year dummies indicate that 1988 and 1990 were particularly good years for the northern fishery, whereas 1989 and 1990 were good for the southern fishery. The fluctuations from year to year are quite significant: for example, the 1989 yellowfin tuna vessel catch level in the southern fishery was more than double that in the base year, holding all other factors constant. These annual fluctuations are partly explained by movements of the East Australia Current. The coefficients on the seasonal dummies suggest that there is little seasonal variation in yellowfin tuna catches for given levels of effort in the northern fishery, whereas in the southern fishery performance in the first quarter of the year is markedly below that in the rest of the year. This pattern is consistent with anecdotal evidence and can be attributed to movements in the East Australian Current (DPIE[2]).

The results indicate that patrolling the longline in the southern fishery increases yellowfin tuna catch by 16%, holding all other factors constant. A 1% increase in soak time was found to increase yellowfin tuna catch by 0.2% in the northern fishery, and 0.08% in the southern fishery. These results perhaps reflect the fact that longer soak times (11.23 h avg.) backed up by patrolling the longline are the norm in the southern fishery, whereas the northern fishery employs shorter soak times (5.96 h avg.). When a hook encounters a tuna, the bait is either removed or the fish hooked. In either case, the hook ceases to fish. Patrolling the line to remove hooked fish and/or rebait will significantly increase catch if there is a significant probability that the rebaited hook will encounter another fish. Since tuna travel in schools, the probability of rebaited hook encountering another fish depends on the probability of the longline encountering another school. It may be that short soaktimes used in the northern fishery make probability of the longline encountering a second school of tuna fairly low. The use of the shorter soaktimes in the north, despite the apparent benefit of an increase in soaktime, may be due to technical factors such as strong currents which rapidly move the line from its point of setting.

The results suggest that in the northern fishery purpose-built longliners and trawlers have a significant catching advantage over multipurpose vessels and planing longliners. For example, holding all other factors constant, a purpose-built longliner will have a 64% higher yellowfin tuna catch, and a trawler a 33% higher yellowfin tuna catch than a planing longliner. Against this advantage in yellowfin tuna catch performance must be set any disadvantage in terms of higher costs of operating these vessels. However, a survey by Campbell and McIlgorm (1992) revealed that the cost per unit of effort for planing longliners was around 1.8 times that of multipurpose vessels and trawlers. Cost data were not available for purpose-built vessels.

SST recorded by fishermen constituted a significant variable in both fish-

Table 1.—Results of the regression for the period 1987–90.[1]

Variable	North	South	Variable	North	South
A (Constant)	0.874** (2.28)	0.756* (2.57)	q_2 (Season 2)	0.285*** (1.72)	0.382* (5.17)
a (Patrol)	N/A[2]	0.151* (3.50)	q_3 (Season 3)	−0.235 (−1.36)	0.365* (5.80)
m_1 (New moon)	0.107 (1.42)	N/A	y_1 (1988)	0.464* (5.04)	0.285* (4.16)
m_2 (First phase)	−0.104 (−1.36)	N/A	y_2 (1989)	−0.036 (−0.47)	0.766* (12.22)
m_3 (Full moon)	−0.047 (−0.62)	N/A	y_3 (1990)	0.263* (3.19)	0.488* (7.09)
c_1 (Multipurpose)	0.077 (0.89)	N/A	δ (lnSt)	0.201* (4.12)	0.08* (2.88)
c_2 (Trawlers)	0.285* (4.28)	N/A	α (ln effort)	0.724* (11.65)	0.535* (10.59)
c_3 (Purpose built)	0.498** (2.37)	N/A	γ (Temperature)	−0.106* (−4.39)	−0.068* (−3.65)
q_1 (Season 1)	−0.141 (−0.79)	0.407* (7.83)	Summary statistic: R_2 north = 0.267, south = 0.138. Sample size (n) = 1,412 (north) and 2,448 (south).		

[1] * = t significant at 1% level, ** at 5% level, *** at 10% level (t ratios in parenthesis).
[2] N/A = not applicable.

eries. In the north an additional 1° more or less than the optimal temperature reduced yellowfin tuna catch by 11%, whereas in the south the estimated reduction is 7%. This confirms the view that local movements of yellowfin tuna stocks are influenced by water temperature variations, and that information on water temperature is important in the conduct of the fishery.

The constant term in each production function represents the log of catch for base values of the dummy variables, without taking into account the effects of soak time, water temperature, and local stock depletion caused by the level of individual vessel effort. It can be used to calculate a base level of yellowfin tuna catch per unit of effort (CPUE) in each fishery for assigned values of the soak time, temperature, and effort variables. When effort and soak time are assigned their mean values, water temperature assumes its optimal value, and all dummy variables are set equal to zero, it can be estimated that 277 hooks set in the northern fishery yield 201 kg of yellowfin tuna and 345 hooks in the southern fishery yield 59 kg. The corresponding CPUE estimates are 0.73 kg per hook in the north and 0.17 in the south. This comparison understates the relative performance of the southern fishery since, as can be seen from the positive signs of the coefficients of the season and year dummies, the base period chosen for the comparison is the worst season in the worst year of the sample for the southern region. However, the comparison can also be carried out for the best season in the best year for each region, and allowing vessels in each region to adopt those fishing practices identified by the analysis as advantageous. When this is done the CPUE is 2.53 kg in the north, and 0.64 kg in the south. Thus the northern region appears to have a fourfold advantage over the south in terms of CPUE.

The coefficient on the log of effort is an estimate of the percentage increase in yellowfin tuna catch per vessel in response to a 1% increase in the level of effort. Again the comparison of the northern and southern fisheries favors the north: a 1% rise in vessel effort produces a 0.72% rise in yellowfin tuna catch in the northern fishery and a 0.54% rise in the southern fishery.

The comparison of the northern and southern fisheries suggests that a shift of vessel effort from the south to the north would increase total yellowfin tuna catch. This result may reflect the fact that the southern fishery is operating close to the limit of the distribution of yellowfin tuna in the South Pacific Ocean.

Conclusion

In summary, the analysis of the 1987–90 sample provided some evidence of seasonal and annual fluctuations in performance: season 2 (July–September) was clearly best in the north, whereas season 4 (January–March) was clearly worst in the south; 1987 and 1989 were the worst years in the north, and 1987 was the worst in the south. Moon phase was of no significance in the south and of little significance in the north.

Some fishing practices appeared to provide a relative yellowfin tuna catching advantage. The use of trawlers and purpose-built vessels provided higher catch rates in the north, holding other factors constant. Patrolling the longline resulted in a significantly higher catch in the south but not in the north. Soak time is important in both fisheries, but more so in the north where there appear to be significant gains to longer soak times; these apparent gains might be offset by operational difficulties resulting from drifting of the longline. In both regions of the fishery placing the longline in waters close to 21.5°C results in significantly higher catch rates.

Overall, the northern region seemed to provide significantly higher yellowfin tuna CPUE. Furthermore, the predicted response of catch to an increase in effort per vessel was more favorable in the north than the south. This suggests that consideration might be given to developing the northern fishery further.

Acknowledgments

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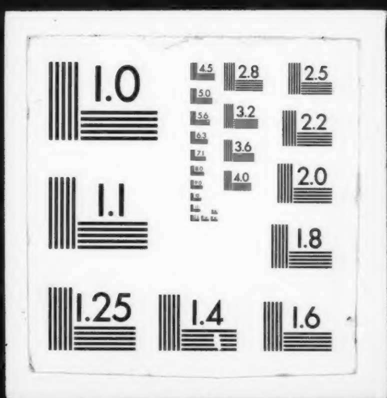
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